Intake and digestibility studies with captive African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

by

Dirk Gerber Borstlap

Dissertation submitted to the Faculty of Natural and Agricultural Sciences,
Department of Animal, Wildlife and Grassland Sciences,
University of the Free State,
in fulfilment of the requirement of the degree Magister Scientiae Agriculturae.

Supervisor:	Prof. H.O. de Waal (University of the Free State)
Co-supervisor:	Dr L.M.L. Schwalbach (University of the Free State)

African Large Predator Research Unit
ALPRU

Bloemfontein, November, 2002

Declaration

I hereby declare that the dissertation submitted by me to the University of the Free State for the degree, **Magister Scientiae Agriculturae**, has not previously been submitted for a degree to any university. I further cede copyright of the dissertation in favour of the University of the Free State.

Borstlap

Dirk Gerber Borstlap
Bloemfontein
November 2002

For my parents Leon and Isabel Borstlap

Acknowledgements

Thank you to the Heavenly Father who has blessed me with the grace, strength and ability to complete this study.

The author wants to express his gratitude to the following people:

Prof. H.O. de Waal, the supervisor of this study for his constant help and guidance. It was indeed a great honour to be one of his students and share in his knowledge and experience.

Dr. L.M.L. Schwalbach, the co-supervisor for his valued advice regarding this study. His help, advice and friendship is greatly appreciated.

Mr. Mike Fair for the advice regarding the statistical analyses.

Mr. W.J. Combrinck for his help in the laboratory regarding the analysis of the samples.

Mr. S.J. van der Merwe, curator of the Bloemfontein Zoological Gardens, Mangaung Local Municipality for allowing me to use the animals and facilities to conduct this study.

The National Research Foundation (NRF) for the financial assistance.

Mr. D.J. Barnes, Mr. R. Vertue, Mr. A.A. Kriel, and the staff of the Bloemfontein Zoological Gardens for their technical help and advice regarding the feeding and caring for the animals.

Yanna Smith for her contribution to the study.

Mrs. Hesma van Tonder for her help with the searching of the references.

The Soetdoring Nature Reserve for their friendly donation of a horse carcass.

My parents, family and friends for their moral support and encouragement.

Table of Contents

1 Introduction

The reproduction, social behaviour and habitat of the large African predators have been extensively researched, as well as the impact on the numbers of their prey species. Similarly, the feeding habits and prey preferences of the predators have also been well studied and documented (Kruuk & Turner, 1967; Schaller, 1972a,b,c; Van Orsdol, 1982; Mills, 1984; Stander, 1992; Viljoen, 1993). Unfortunately, very little is known about the actual quantitative and qualitative nutritional aspects of these well-known animals. Among the wild African predators it is invariably the reproducing females and their young offspring, as well as young nomadic males, who are at greatest risk and affected by the negative impact of nutritional stress.

In Sub-Saharan Africa the numbers of large carnivores have declined during the last 50 years (Stander, 1997). Important reasons for this decline in numbers are the loss of the natural habitat of these animals and the increased conflict with pastoralists (Stander, 1997). The confinement of large carnivores in small areas results in predation of domesticated livestock in certain areas, which leads to further persecution threatening the long-term survival of Africa's large predators. Given the paucity of information on quantitative nutritional aspects, there is a need to improve our understanding of the nutrient requirements and utilization of energy and nutrients by these animals. Similar to domesticated animals, this requires a basic knowledge and understanding of the digestive tract, the processes of nutrient digestion and absorption, as well as nutrient metabolism. This information is needed to make accurate assessments of the actual food intake and ultimately the numbers of specific prey species required for the survival of these large African predators.

The long-term goal of this study on the quantitative nutrition of large African predators is to develop non-invasive techniques for the accurate determination of food intake and apparent nutrient digestibility by free-ranging predators. In the development of such non-invasive techniques, the first phase of the research programme embodied in this study was conducted on three species of captive large African carnivores. For obvious reasons this first phase was done with captive predators in order to have a reasonable measure of control over the environment and procedures where the food intake and faecal excretion of the predators could be determined as accurately as possible. Although the study was done with captive animals, every effort was made to ensure that these techniques were developed in such a manner that the principles would be applicable in the uncontrolled natural environment of the free-ranging African predators.

The specific objectives of this study were to:

1. develop non-invasive techniques to determine the apparent digestibility of fresh, non-processed food by three species of large African predators.
2. determine the apparent dry matter (DM) digestibility of typical carnivorous diets in terms of DM, crude protein (CP), minerals, fat and gross energy (GE).
3. obtain information on the digestive capabilities and the water retention in three species of large African predators.
4. lay the basis for developing a technique to determine the food intake on a nutrient basis by free-ranging large African predators.

2 Literature review

In the following focussed literature review, only certain specific aspects regarding the nutrition of African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) are discussed.

Very little is known about the digestive capacities of large African predators in general. A small number of studies have been reported by Morris *et al.* (1974) and Barbiers *et al.* (1982) on the digestion of diets by large African felids. Recently the intake and digestibility of a red hartebeest (*Alcelaphus buselaphus*) hindquarter and the hind and fore limbs and the skin of donkeys (*Equus asinus*) were determined with lions at the Bloemfontein Zoo (Yanna Smith & H.O. de Waal, 2001; personal communication). Except for these reports no information is available on the digestion, rate of passage, retention time of food in the alimentary canal and the absorption of nutrients by large African predators in a scenario that closely resembles the feeding environment in the wild.

The word *Carnivora* literally means "meat eaters" and the order Carnivora consists of animals with specific adaptations to perform the actions necessary to kill prey animals and eat the meat. The carnivores have retained a versatile array of dentition adapted cutting meat, crushing bone, and even for the grinding of insects (Van Valkenburgh for holding prey,, 1989). The teeth of different carnivores are adapted for specific functions and types of food. The teeth of carnivores are generally developed to punch and tear through skin, crush bone and cut meat. The teeth are particularly well developed for this task. According to Skinner & Smithers (1990) the dental formulae of the lion, leopard and cheetah are the same, namely:

$$I\,\frac{3}{3}\quad C\,\frac{1}{1}\quad P\,\frac{3}{2}\quad M\,\frac{1}{1}\quad = 30$$

The huge canines and canine-like upper and outer incisors are adaptations to the need for holding and strangling heavy prey. The remainder of the teeth is adapted to slicing up the meat. The molars have little grinding ability, but help to prevent tough food from sliding back during feeding (Van Valkenburgh, 1989; Skinner & Smithers, 1990).

An examination of the alimentary tracts of lions (H.O. de Waal & W.J. Combrinck, 2001; personal communication) showed that the relatively simple, short and small alimentary canal appears to be capable of efficiently obtaining and retaining nutrients from their diet. The total length of the alimentary canal, excluding the 9 cm of the ceacum, was about 9 m and the total volume 11.15 litre (H.O. de Waal & W.J Combrinck, 2001; personal communication). The same simplicity in the alimentary tract witnessed in the lion is expected in the leopard and cheetah.

Meat is a highly nutritious food source and consists of water, proteins, lipids (fats), carbohydrates, minerals and vitamins. Most muscle foods contain between 150 and 350 g protein/kg food on a fresh basis (Godber, 1994). This protein content may vary according to the fat and water content of the meat. According to Godber (1994) the fat content of meat is the most variable component and varies between 100 and 400 g/kg for red meat. According to McDonald *et al.* (1995) animal fat and muscle contain 39.3 MJ/kg DM and 23.6 MJ/kg DM respectively. Carbohydrates are stored in muscle as the "animal starch", glycogen (McDonald *et al.*, 1995). Glycogen is the main carbohydrate storage product in the animal body and consists of long polymers of α-D-glucose residues (McDonald *et al.*, 1995). There is usually very little glycogen left in muscle when consumed as food, usually less than 50 g glycogen/kg food on a fresh basis (Godber, 1994). This is especially true after an energy-consuming chase has occurred during which a prey animal has been run down, caught and killed by a predator. Meat is a fair to good source of the vitamin B complex and a fair to good source of all the fat-soluble vitamins. Meat is also a good source of minerals, especially iron, phosphorus, copper and manganese. Muscle is generally low in calcium, but bone and blood plasma have high calcium contents (McDonald *et al.*, 1995).

Meat contains large quantities of water and, therefore, the digestibility of animal carcass portions will vary considerably (H.O. de Waal, 2002; personal communication). Recently trials were conducted on the digestibility of the hindquarter of a Red Hartebeest (*Alcelaphus buselaphus*) and diets consisting of a fore and hind limb and the skin of donkey stallions by captive lions (Yanna Smith & H.O. de Waal, 2001; personal communication). These studies were conducted on the assumption that lions do not eat on a daily basis, thus mimicking the infrequent feeding conditions in the wild. The experimental diets were also intact and not ground as was done in other studies (Morris *et al.*, 1974; Barbiers *et al.*, 1980), to allow for the eating and chewing processes of lions, leopards and cheetahs. These studies (Yanna Smith & H.O. de Waal, 2001; personal communication) were conducted at the level of the gross carcass components only, namely portions of the carcasses were dissected into meat, bone and skin. Except for determining the DM content, no nutrient analyses of the diets, food refusals or faeces were conducted.

Cats are intermittent feeders and can go without food for long periods at a time, provided they are adults and not nursing young. Cats are essentially lazy animals and will only work for food when hungry (Scot, 1998). This entails that when predators and especially cats have a meal, whether it originated from prey being killed or scavenged, maximum use must be made of the food in terms of nutrient and energy digestion and absorption. In order to digest and absorb the maximum amount of nutrients and energy from their diets, the digestive tract and the feeding apparatus must be equally well adapted to perform the necessary tasks in killing prey, eating and digesting typical carnivorous diets.

2.1 The African lion (*Panthera leo*)

The lion (*Panthera leo*) is the largest of the African carnivores (Skinner & Smithers, 1990). Lions grow rapidly during the first three years of their lives and thereafter the growth rate slows down. The size of lions is related to food intake and genetics and therefore varies from region to region (Bothma & Walker, 1999). The average mass of lion males in the Kruger National Park is 190 kg and that of the females is 126 kg (Skinner & Smithers, 1990).

African lions (*Panthera leo*) are nocturnal and crepuscular and hunt mainly at night (Schaller, 1969; Bertram, 1975; Schaller, 1972a; McBride, 1982; Bothma & Walker, 1999). Lions eat any suitable food and maintain a large variation in diet throughout their geographic area (Bothma & Walker, 1999). Lions are not exclusively predators, but scavenge a large proportion of their food (Kruuk & Turner, 1967; Schaller, 1969; Skinner & Smithers, 1990; Bothma & Walker, 1999). The lions living on the *Acacia* savannah of the Serengeti National Park, Tanzania hunt and kill 83% of their food, while those living on the open plains scavenge 53% of their food (Bothma & Walker, 1999). In North-eastern Namibia, lions killed 96.3% of their food and scavenged only 3.7% (Stander, 1997).

Lions eat a wide range of mammals from mice to buffalo, birds to the size of an ostrich (*Struthio camelus*) and even reptiles and insects (Skinner & Smithers, 1990). Lions, however, seem to eat more prey ranging from 20 kg in size to the Cape buffalo (*Syncerus caffer*), which falls in the 800 kg class (Eloff, 1973; Skinner & Smithers, 1990; Bothma & Walker, 1999). It was recorded that in the Kaudom Game Reserve and the Tsumkwe district in North-eastern Namibia, 92% of the observed lion kills comprised of kudu (*Tragelaphus strepsiceros*), giraffe (*Giraffa camelopardalis*), gemsbok (*Oryx gazella*) and wildebeest (*Connochaetes taurinus*) (Stander, 1979). In isolated cases livestock is taken (e.g. cattle, horses and donkeys), but natural prey was preferred rather than livestock (McBride, 1982). Crocodiles (*Crocodylus niloticus*), baboons (*Papio ursinus*) and guinea fowl (*Numida meleagris*) and sometimes even other lions also fall on the lion's menu (Pienaar, 1969). Lions, however, tend not to concentrate on small animals such as birds, hares and small antelope such as dik-dik (*Madoqua kirkii*) due to the enormous energy output required during the charge and kill versus the marginal energy gain from these prey (Schaller, 1972a). Kruuk & Turner (1967) noted that wildebeest comprised about 50% and zebra about 25% of the number of animals killed by lions in the Serengeti. The largest proportion of kills made by lions comprises young, sub-adult or small animals (Eloff, 1973; McBride, 1982).

Lions may hunt as individuals or in groups (Kruuk & Turner, 1967). Well-fed lions will hunt in large groups, thereby limiting the expected number of chases needed to meet their daily nutritional requirements (Clark, 1987). Hungry lions will hunt in smaller groups to maximise the food intake per individual (Clark, 1987). Lions hunt by stalking its prey (Bertram, 1975). The hunting success of lions varies from area to area depending on the terrain, pride size, prey composition and abundance (Bothma & Walker, 1999). The hunting success of lions ranges from between 15% in the Etosha National Game Reserve to 61% in the Serengeti (Bothma & Walker, 1997).

Lions are adapted to a "feast and famine" feeding regime. They can ingest enormous amounts of food, eating the skin, meat and viscera, that is almost everything except the large bones and the stomach contents (Schaller, 1969). In the wild the amount of food ingested during a feeding may vary quite considerably. A once off intake 33 kg of meat has been reported for a male lion (Schaller, 1969). In a study by Smuts (1978) most of the stomach contents of the adult lions that were dissected, were less than 15% of true body mass. Lions can go for long periods without food, but when food is available they can consume huge quantities of meat

(Eloff, 1973). The amount of food ingested during a feeding may vary quite considerably. The estimated intake of food of lions is between 4.7 and 14 kg per day and may exceed 40 kg or 25% of their own body mass (Schaller, 1969; Eloff, 1973; Van Orsdol, 1982; Clark, 1987; Packer *et al.,* 1990; Stander, 1992; Mills & Biggs, 1993). Packer *et al.* (1990) estimated a daily food requirement of 5 to 8.5 kg for survival. Males ingest twice as much food as females when they are eating from the same carcass (Packer *et al.*, 1990). The food intake of lions varies according to season and prey availability (Van Orsdol, 1982; Viljoen, 1993).

The feeding interval of lions is not constant and may vary considerably. The lions in the Kruger National Park have a mean feeding interval of four days (Smuts, 1979). Van Orsdol (1982) reported a mean feeding interval of 3.1 days in the Rwenzori National Park, Uganda. Similar feeding intervals were reported in the Serengeti National Park, Tanzania (Schaller 1969). However, the feeding interval may be as short as one day (Bothma & Walker, 1999). The maximum length of a feeding interval reported in the Kruger National Park is 13 days (Smuts, 1979; Bothma & Walker, 1999). This means that lions are adapted to a feast and famine lifestyle (Schaller, 1969); hunting and eating only when hungry and being able to catch prey while lying around and resting in the shade of trees the rest of the time.

When food intake is expressed as the estimated daily intake, it might create the impression that lions eat every day, which is not the case. Furthermore, the food intake of lions is invariably expressed on an as fed or fresh basis with a very high but unknown water content (H.O. de Waal, 2002; personal communication).

Lions that hunt alone in the prey-poor dry season of the Etosha National Park in northern Namibia, do not get the estimated minimum food intake of 5 to 8.5 kg fresh food required for survival and therefore experience nutritional stress at times (Packer *et al.*, 1990; Stander, 1991). Lions may also on occasions kill twice as much food as what is needed for survival and the excess is left to feed the scavengers (Wright, 1960, as quoted by Eloff, 1973).

Lion cubs also eat meat and grow more rapidly when an abundance of prey is present. Lion cubs show interest in other animals at the age of five months but only start hunting at about 11 months (Bothma & Walker, 1999). In captivity lion cubs have been observed chewing on meat at the age of two to three months (Daryl Barnes, 2002; personal communication). Lion cubs are weaned after a long lactation period from the age of 6-12 months (Skinner &

Smithers, 1990; Bothma & Walker, 1999). Cubs eat more meat than adult lions in relation to their size (Smuts, 1979; Bothma & Walker, 1999). It was reported by Smuts (1978) that it is quite common for the stomach contents of cubs to exceed 20% of their body mass while the highest value observed in adult and sub-adult lions was 17%.

Typical diets of lions consist of muscle, bone, cartilage, fat, skin, organs, digestive tract and intestinal contents, blood and other body fluids, feathers, quills of porcupines and some plant material (H.O. de Waal, 2002; personal communication). Smuts (1978), reported that pieces of horn and teeth, together with other body parts were found in the stomach contents of lions. In addition to the remains of prey animals, plant material was often found in the stomachs of lions. Depending on the time of year, green grass was supposedly picked up and ingested by accident while feeding (Smuts, 1978). However, it was found by Smuts (1978) that a female lion ingested about 200 g of green grass and the stomach only contained a small amount of impala meat (*Aepyceros melampus*). Traces of soil were frequently found in the stomach contents of lions (Smuts, 1978), probably as the result of contamination of the prey animal carcass with soil during the feeding process.

Smuts (1979) suggested that, although stomach morphology may be involved, a higher metabolic rate of cubs might be the cause of the higher food intake. This may be true because the cubs need a higher supply and flow of nutrients to provide the higher nutrient requirements for growth. Furthermore, cubs are at the bottom of the feeding hierarchy of the pride and need to ingest as much meat as possible when a meal is available, to survive. Bothma & Walker (1999) and Eloff (1980) also pointed out that although cubs survived for long periods between suckling on the rich milk provided by the lionesses, cubs may still die of malnutrition and starvation in prey-poor areas. This is especially true in prey-poor areas where the mother is absent from her cubs for as long as two to three days (Bothma & Walker, 1999). Although cubs eat meat from an early age, they only show interest in prey species at an age of five months (Bothma & Walker, 1999). The growth and development of lions as in other animals, is greatly dependent on adequate quantities and quality of food. Lions are often stunted due to inadequate food intake (Smuts *et al.*, 1980).

Lions eviscerate the carcass of the prey before feeding (Skinner & Smithers, 1990). They may eat some bone, but muscle is their main food (Bothma, 1997). The intestines are sometimes buried or covered with sticks and grass. Sometimes the intestines are eaten after being drawn through the incisors to squeeze out the contents (Skinner & Smithers, 1990). In some cases as in the Kalahari, lions may bury the viscera in the sand and eat the remainder of the carcass somewhere else (Eloff, 1977; Bothma, 1997). The quills from porcupines (*Hystrix africaeaustralis*) are removed to a fair extent before eating the carcass. Mortalities do occur when lions attempt to kill and eat porcupine (*Hystrix africaeaustralis*) due to external injury inflicted by the quills (Bothma, 1997; Bothma & Walker, 1999). The alimentary canal of the African lion is very simple and short, therefore, porcupine quills will pass relatively easy through it and be excreted in the scat (H.O. de Waal, 2002; personal communication). This refutes the statement by Eloff (1999) that lions must have a high threshold for pain to allow the passage of large quantities of porcupine quills through the alimentary tract with its many bottlenecks.

Lions are not good parents and the mortality among cubs is high (Schaller, 1969). Cubs are dependent on adults until at least the age of 16 months and usually until the first 2½ years of life. Eloff (1980) observed cubs dying of malnutrition and starvation, showing symptoms of rickets. Lactating lionesses need more food than provided by small prey like porcupine (*Hystrix africaeaustralis*) or other small mammals to keep up with the nutritional requirements of lactation.

In many areas in Africa, 66-75% of lion cubs die before reaching the age of one year (Eloff, 1999). The reason for these high mortalities is mainly caused by nutritional factors. In some cases the lionesses do not get enough nutrients to satisfy the increase in nutritional demand for the production of milk for the cubs. Other reasons include diseases, predation and neglect (Eloff, 1999). The nutrition of the females is therefore of utmost importance to ensure the survival of cubs and also to be able to provide in the demand for meat by the pride.

2.2 The leopard (*Panthera pardus*)

The leopard (*Panthera pardus*) is the only large wild cat that can survive near human habitation (Bothma & Walker, 1999). The mean weight of adult leopards is about 60 kg for males and about 32 kg for a female (Skinner & Smithers, 1990). However, adult male leopards may weigh up to 90 kg and females up to 60 kg in some areas. The mean weight for males in the Kruger National Park is 58 kg and 37.5 kg for females (Bothma & Walker, 1999). The leopards in the coastal mountain areas are much smaller. The males and females weigh 31 and 21 kg respectively (Bothma & Walker, 1999).

In the Kalahari, leopard males kill every three days and leopard females with cubs kill twice as frequently (Skinner & Smithers, 1990). In Namibia it has been documented that with cubs females without cubs eat 1.6 kg and those with cubs eat 2.5 kg, while males eat 3.3 kg of meat per day (Bothma & Walker, 1999). Leopards, like most predators will eat almost any prey that is available. The diet of leopards is more varied than the diet of cheetah and lion (Schaller, 1972b). Leopards have even been observed eating the beetles out of buffalo dung (Bothma & Walker, 1999) and fish (Skinner & Smithers, 1990; Bothma, 1997). Although leopards are highly adaptable, ungulates comprise the major part of the diet. Unlike lions, leopards often kill and eat other predators. Wild dogs (*Lycaon pictus*), cheetahs (*Acinonyx jubatus*), bat-eared foxes (*Otocyon megalotis*) and lion cubs are among the predators killed by leopard (Bothma & Walker, 1999). Leopards generally do not attack each other as prey, but eat from the kill of other leopards. In isolated cases, however, leopards may be cannibalistic (Bothma, 1997).

In southern Africa the mean prey size for leopards vary between 20 kg and 70 kg (Bothma, 1997). The size of most of the prey species (76%) falls in the small category (20-100 kg). Kills in the medium sized range (100-350 kg) account for only 7% of all kills. Because leopards hunt from cover, small animals that usually occur on open plains are seldom caught (Kruuk & Turner, 1967). Leopards hunt by ambushing and stalking its prey. Among other prey often killed by the leopard for food are porcupine (*Hystrix africaeaustralis*), duiker (*Sylvicapra grimmia*) and gemsbok (*Oryx gazella*). Other predators like the black-backed jackal (*Canis mesomelas*), bat-eared foxes (*Otocyon megalotis*) and the aardwolf (*Proteles cristatus*) are also frequently killed and consumed by leopards (Bothma, 1997). According to Schaller (1972b), leopards killed a total of 24 other species of predators. Birds and rodents are also quite often killed and eaten by leopards. Leopards have also managed to kill eland bulls (*Taurotragus oryx*), the largest antelope species in Africa (Bothma & Walker, 1999). In some areas with rocky outcrops, for example in Matobo National Park, Zimbabwe, where rock hyraxes (*Procavia capensis* and *Heterohyrax brucei*) are abundant, these animals may account for 55% and 61% of the stomach contents of leopards in those areas (Bothma, 1997). In the Serengeti the diet of leopards include python, hyrax, hare, and various small and medium sized antelope (Schaller, 1972b).

In some areas in the African savannah, impala (*Aepyceros melampus*) is an important and staple prey source for leopards. Leopards will also occasionally eat fruit like the tsama melon (*Citrullus lanatus*) and the gemsbok cucumber (*Acanthosicyos naudianus*), supposedly more for its moisture than as an energy source (Bothma & Walker, 1999). Impala (*Aepyceros melampus*) has accounted for 88% of the kills made by leopards in the Klaserie Private Nature Reserve (Bothma, 1997).

Leopards prefer to hunt at night, but kills also occur in the early hours of the morning and in the late afternoon (Schaller, 1972b). Like the other cats, leopards kill by strangulation. Hunting is opportunistic and hunger is the basic motivation for leopards to hunt (Mills, 1984; Bothma, 1997). Like lions, leopards may be classified as fairly unsuccessful hunters. In the Kruger National Park, only 16% of all leopard hunts are successful (Bothma & Walker, 1999).

When leopards start to feed it usually eviscerates the prey at the kill site and carries or drags it to suitable cover (Bothma & Walker, 1999). Small prey may be consumed entirely at the kill site. The distance over which a kill may be moved may vary quite considerably. In the African bushveld the distance seldom exceeds 100-200 m. In the Kalahari, however, the distance may exceed 4.2 km (Bothma & Walker, 1999). The removed viscera may or may not be covered with sand or litter. Before feeding, the leopard usually uses its incisors to remove the hair or fur of the prey animal and leave it in a neat pile (Bothma & Walker, 1999). Feathers and quills of birds and porcupines are also removed in the same manner (Skinner & Smithers, 1990). The tongue is used to rasp meat off the bones much in the same way as lions do. Feeding normally starts at the buttocks, chest or shoulder of the prey (Bothma & Walker, 1999). The muzzle, lower jaw, viscera and feet are usually not eaten.

Leopards are known to cache food in trees (Skinner & Smithers, 1990; Bothma & Walker, 1999). The reasons for this may be to avoid interference from other predators and in some cases the prey may be too big to consume in one day. If the leopard is not robbed from its food, it may take up to six days to consume the carcass of a large kill.

Leopards also show great adaptability in their hunting techniques according to the availability of prey, differences in the defensive capabilities and the degree of hunger that the leopard is experiencing (Bothma & Le Riche, 1989).

Leopard cubs are totally dependent on the mother for the first 12 months (Bothma & Walker, 1999). Leopard females may leave cubs alone for up to six consecutive nights when hunting is not successful, leaving the cubs highly susceptible to starvation and predation (Bothma & Walker, 1999). Cubs are presented with meat at 65 days of age but start eating meat at 72 days of age and are weaned at 101 days (Skinner & Smithers, 1990). Cubs are usually led to a kill at the age of nine and a half months (Skinner & Smithers, 1990). At 11 months of age cubs accompany their mother on the hunt for the first time (Skinner & Smithers, 1990). They generally leave the mother at the age of 12-18 months, siblings remaining together in a group for a further 2-3 months (Skinner & Smithers, 1990; Bothma & Walker, 1999).

2.3 The cheetah (*Acinonyx jubatus*)

The cheetah (*Acinonyx jubatus*) is the most specialised of all the 37 cat species (Marker *et al.*, 1999). As the fastest land mammal, it can reach speeds of up to 110 km/h and is built for speed and agility rather than power, like the other big cats (Marker *et al.*, 1999). Superficially a cheetah has a more dog-like appearance, but it is a true cat closely related to the lynx, lion and tiger (Bothma & Walker, 1999). Adult cheetahs weigh on average between 40 and 60 kg (Skinner & Smithers, 1990). The modern cheetah (*Acinonyx jubatus*) is an eastern hemisphere (Old World) species, a region where at least two other species existed. Unfortunately the cheetah is now on the list of endangered species. Namibia has the largest remaining number of free-ranging cheetah (Marker *et al.*, 1996).

Cheetahs hunt mostly at daytime with the highest activity during the early morning and late afternoon (Kruuk & Turner, 1967; Schaller, 1972a; Eaton, 1974; Skinner & Smithers, 1990). This is presumably true because cheetahs rely greatly on their eyesight for hunting. According to Bothma & Walker (1999) cheetahs in general require between 3-4 kg of meat per day to remain in top condition. The principal prey species are small and medium sized animals of less than 60 kg (Skinner & Smithers, 1990)

According to Bothma & Walker (1999) the prey species also differ according to the area and the availability of a particular species. In the Serengeti, Thomson's gazelle (*Gazella thomsoni*) accounts for 91% of cheetah kills. In the Kruger National Park, impala (*Aepyceros melampus*) comprises 68% of all cheetah kills. Cannibalism is rare in cheetah and may occur in isolated cases (Bothma & Walker, 1999).

Animals such as springbok (*Antidorcas marsupialis*) are hunted with a success rate of 58.5% while the larger and significantly more dangerous oryx (*Oryx gazella*) is hunted with a 14.3% success rate (Bothma & Walker, 1999). In Namibia, kudu calves (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), warthog piglets (*Phacochoerus aethiopicus*) and steenbok (*Raphicerus campestris*) are the main prey species of cheetah (Marker *et al.*, 1996).

The success rate of cheetah hunts, like that of the other predators, vary according to a number of factors, e.g. prey availability, cover provided by vegetation as well as age and size of the prey. In the Nairobi National Park, Kenya cheetahs kill all their prey species combined with a success rate of 37%. Juvenile prey is hunted at a greater success rate of 76%. The hunting success of a female with cubs is around 41% (Bothma & Walker, 1999). Cheetahs, like other predators, appear to take the younger and more vulnerable animals in the herd (Mills, 1984).

Cheetahs eat hurriedly to avoid losing the kill to other predators and can consume up to 14 kg of food in one sitting (Schaller, 1972b; Marker *et al.*, 1996; Bothma & Walker, 1999). When eating, cheetahs usually start at the buttocks and ribs (Skinner & Smithers, 1990; Bothma & Walker, 1999). The heart and liver are regularly eaten while the intestines are pulled out and generally not eaten (Skinner & Smithers, 1990; Bothma & Walker, 1999). The blood accumulating in the body cavity is lapped up as an additional source of nutrients and water. The larger bones and skin are usually not eaten. Cheetahs over six months will crush and eat the soft bones of young prey animals (Bothma & Walker, 1999). Cheetahs are not scavengers (Schaller, 1972b). However, a case of cheetahs scavenging on a 2-year old wildebeest that died of unknown causes was documented in the Serengeti (Caro, 1982). It must however be noted that the carcass was very fresh and no other scavengers such as vultures or hyaenas had visited it prior to the cheetahs.

In the wild cheetahs are not restricted to a breeding season (Skinner & Smithers, 1990). The availability of food greatly influences cheetah reproduction. Cubs stay with the female for almost a year (Skinner & Smithers, 1990). During the first 12 months of the life of cubs the female cheetah is in the most critical stage in terms of nutrient requirements, because not only does she need to fend for herself, but for her young as well. Cheetah cubs start eating meat at 5-6 weeks of age and begin the weaning process at six weeks and are usually weaned at three months (Eaton, 1974; Skinner & Smithers, 1990). Cheetah cubs start to hunt actively from the age of 8-12 months (Skinner & Smithers, 1990).

Cheetahs in the wild have a high mortality rate. The cubs are especially plagued by death at an early age. According to Bothma & Walker (1999) up to 72% of all cubs born, die before they emerge from the den at six to eight weeks of age. The main cause of death of cubs is predation by other predators. According to Bothma & Walker (1999) 50% of all cubs in the Serengeti are killed by lions, leopard and hyaena (*Crocuta crocuta*) before they reach eight months of age. In the Kalahari, 50% of cubs are killed by starvation and predation before they reach six months of age. Cubs are also prone to starvation in the den when the mother is off stalking migrating herds of antelope. Cubs may also join reluctant groups of other cheetahs and steal food from them in order to survive. Cheetah females in captivity have been known to regurgitate food for their cubs, but this has yet to be observed in the wild (Bothma & Walker, 1999).

2.4 Water requirements

Little is known of the water requirements of wild carnivores and especially those adapted to desert conditions. The diet of these carnivores is relatively high and constant with respect to its water content (Green *et al.*, 1984). The water content may account for 85% of the total mass of prey animals' bodies (Green *et al.*, 1984). Predators may therefore obtain sufficient water to survive for some time from the blood and soft tissue of prey animals. Lions, leopards and cheetahs will drink water regularly when available (Eloff, 1973; 1999; Green *et al.*, 1984; Bothma & Walker, 1999).

When water is not available, lions, leopards and cheetah have been known to go without water for long periods at a time. These predators can even survive without free water (Bothma & Walker, 1999). It appears that lionesses with cubs have a greater need of water to keep up with milk production (Eloff, 1973). The same can be expected with leopards and cheetahs.

Lions, leopards, cheetahs as well as other predators have been known to eat the tsama melon (*Citrullus lanatus*) and the gemsbok cucumber (*Acanthosicyos naudianus*) to utilise its high water content (Eloff, 1999; Bothma & Walker, 1999). Rainwater may also be licked from the pelt in order to obtain some water (Eloff, 1999). Female leopards seldom drink water, even when they have cubs (Bothma, 1997).

3 Material and Methods

An important aim in conducting these non-invasive food intake and digestibility studies with the large African predators was to ensure that the feeding routines to which the captive animals were accustomed in the Bloemfontein Zoo would not be disrupted. The customary feeding routines were followed and adhered to as far as possible to avoid upsetting the general daily routines of the animals.

3.1 Study environment

The study was conducted in the Bloemfontein Zoological Gardens (Bloemfontein Zoo) with pairs of male and female captive lions, leopards and cheetahs. The facilities in which the pairs of large predators per species are housed (Figure 3.1) consist of brick and concrete enclosed night chambers (2.35 m x 2.6 m and 5.65 m x 2.6 m), separated by steel grate trapdoors from an open-air leisure yard. The leisure yards measure about 729 m^2, 432 m^2 and 513 m^2 for the lions, leopards and cheetahs respectively. The male and female of each species shared a facility. The leisure yards are planted with Kikuyu grass (*Pennisetum clandestinum*) as ground cover and further naturalised or landscaped with large rocks and tree trunks. The steel trapdoors are remotely controlled by a system of pulleys and cables to protect the operators from the predators.

The large predators in the Bloemfontein Zoo are accustomed to a strict feeding routine. The lions are fed on Sunday and Wednesday afternoons at about 14h30. The leopards and cheetahs are fed on Sunday, Wednesday and Friday afternoons at about 14h30. The fresh food allowances per animal per feeding are about 14 to 16 kg of animal carcass for lions and about 5 to 8 kg of animal carcass for the leopards and cheetahs. The diets of the animals used in the trials of this study consisted mainly of portions of donkey and horse carcasses, whole chickens, chicken tripe (intestines, offal meat, skin and fat) and meat from unborn calves or culled game and livestock.

The Bloemfontein Zoo is equipped with a slaughtering facility and a butchery. Cooling and freezing facilities are available in the form of a walk-in freezer and refrigerator operating respectively at –10°C and 4°C. All preparations and storage of trial diets were conducted at this facility.

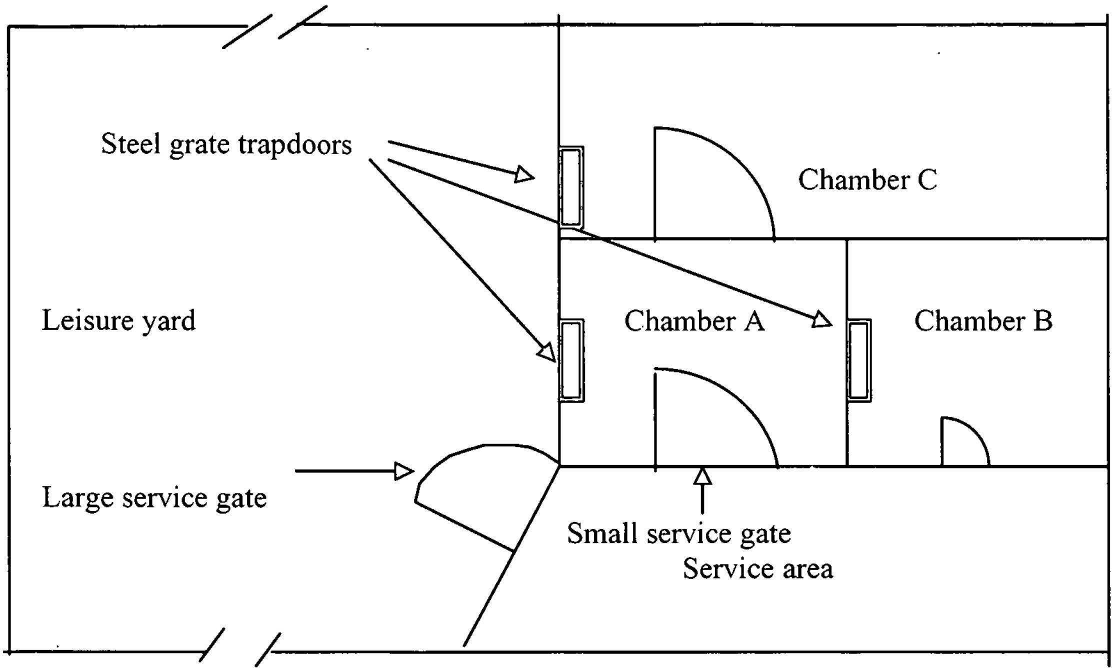

Figure 3.1 Top view of a part of the leisure yard and the brick and concrete night chamber facility (Chambers A, B and C are enclosed night chambers) for large African predators at the Bloemfontein Zoo

3.2 Study animals

The study consisted of 16 complete intake and digestibility trials that were conducted with a male and a female specimen each of three large African predator species.

The following large African predators were used:

- African lions (*Panthera leo*); an adult male and female.
- Leopards (*Panthera pardus*); an adult male and female.
- Cheetahs (*Acinonyx jubatus*); a sub-adult male. Only one intake and digestibility trial could be performed with an adult cheetah female before she was relocated as part of an animal exchange program.

3.3 Study design

In the context of this study, the experimental procedure of conducting a complete intake and digestibility trial was repeated three times with each of the six predators, except in the case of the female cheetah. The design is presented in Table 3.1.

Table 3.1 The design of the study

Trial	Predator	Replication	Date
1	Lion male (*Panthera leo*)	1	27 February 2002
		2	4 March 2002
		3	22 May 2002
2	Lion female (*Panthera leo*)	1	29 May 2002
		2	5 June 2002
		3	9 June 2002
3	Leopard male (*Panthera pardus*)	1	3 April 2002
		2	24 April 2002
		3	5 June 2002
4	Leopard female (*Panthera pardus*)	1	9 June 2002
		2	24 June 2002
		3	26 July 2002
5	Cheetah male (*Acinonyx jubatus*)	1	24 July 2002
		2	26 July 2002
		3	7 August 2002
6	Cheetah female (*Acinonyx jubatus*)	1	1 May 2002
		Not done	
		Not done	

The sequence of trials and replications were randomly decided, based on the availability of animal carcasses.

It should be noted that these replications of the experimental procedure with the respective individual predators (*e.g.* lion male or leopard female, etc.) are referred to as replications 1, 2 and 3 of the trial (*e.g.* Trial 1 or Trial 4 in the case of the example) with the specific individual.

The 16 intake and digestibility trials were conducted during a six-month period from 27 February 2002 until 7 August 2002.

3.4 Weighing of the large predators

The large predators used in the study were weighed at irregular intervals. A steel grid was placed on the two metal beams containing the pressure cells of an electronic livestock scale, designed to weigh cattle. The lions were weighed by placing the steel grid and metal beams of the scale in the leisure yard, immediately in front of the trapdoor leading to the night chamber A (Figure 3.1). The scale was zeroed and the lion simply lured with some food onto the steel grid and the weight recorded. The same procedure was followed with the leopards, except that the steel grid of the scale was put inside the night chambers (Figure 3.1) on the spot where the leopards usually lie down when they are inside the night chambers. The male cheetah was lured into the night chambers and the scale set up outside the chamber just in front of the gate. A steel crate used to transport animals, was put on the steed grid and the scale zeroed. The male cheetah was then lured into the steel crate and weighed. The cheetah female could not be weighed before she was removed in the exchange program with another zoo.

All predators used in the trials were weighed before being fed to avoid fluctuations in body weight due to gut fill. Throughout the trial period every effort was made to avoid as much additional and unnecessary disturbances and stress to the predators as possible, therefore, the weighing procedures were not carried out on a specific animal while an intake and digestibility trial was underway. This fact and the difficulties experienced with the procedure of weighing large predators, even in the excellent facilities of the Bloemfontein Zoo and without the use of immobilising drugs, resulted in each animal being weighed only once. The male and female lions were however weighed on several occasions in previous research projects. During February 2001 the weight of the male and female lions were 182 kg and 137 kg respectively. During May 2001 the weight of the male and female lions was recorded as 171 kg and 121 kg respectively. Given the feeding regime of large predators in the Bloemfontein Zoo, no real large changes in body mass were expected. The body weight of the five large African predators used in this study is shown in Table 3.2.

Table 3.2 Body weight of the five large African predators used in this study

Predator	Male kg	Female kg
Lion (*Panthera leo*)	187.5	129.0
Leopard (*Panthera pardus*)	53.0	35.0
Cheetah (*Acinonyx jubatus*)	40.5	Not weighed

3.5 Trial diets (carcass portions)

The trial diets (carcass portions) were sections or chunks of animal carcasses and consisted of the limbs from either adult donkeys (*Equus asinus*) or horses (*Equus caballus*). These animals were kept on a farm managed by staff of the Bloemfontein Zoo and served as sources of fresh meat for the captive carnivores. Donkeys and horses are fairly easy to obtain and a relatively cheap source of meat in South Africa.

The trial diets used in the study consisted macroscopically of meat, bone, soft and connective tissue as well as skin and hair. This diet composition is very similar to the type of diet these carnivorous animals would consume in the wild. Horses and donkeys, being equine, closely resemble zebra (*Equus burchelli*) a common prey species for many free-ranging large African predators.

Morris *et al.* (1974) reported on the digestibility of a diet preparation comprising horsemeat and meat by-products fortified with minerals and vitamins for carnivores in the Sacramento Zoo, California. The diet fed in that trial, however, comprised small amounts of minced meat (Morris *et al.*, 1974). Similarly, Barbiers *et al.* (1982) conducted studies at the Potter Park Zoo in Lansing, Michigan with a finely ground meat-based commercial diet. In a study done by Powers *et al.* (1989) on bobcats (*Felis rufus*), white-tailed deer meat (*Odocoileus virginianus*), snowshoe hares (*Lepus americanus*) and grey squirrels (*Sciurus carolinensis*) chopped up into five to eight pieces were used as diet. The intestines, skin, bones, head and lower section of the legs of the white-tailed deer were, however, not included in the diet of the bobcats. However, lions in the wild never consume diets of a comparable fineness (minced meat) and/or homogeneity and results obtained in such studies will not apply to the natural scenario where lions ingest large amounts of "unprocessed" food at irregular feeding intervals.

When intake and digestibility studies are performed with any type of animal it is imperative that the exact amount eaten, *e.g.* kg fresh food or preferably expressed as kg DM, as well as the nutrient composition of the carcass, *e.g.* g/kg protein or lipid, is known. Therefore, homogeneous and representative samples are needed for the nutrient analysis to determine the composition of a particular carcass or diet.

There are, however, three major challenges in this regard when dealing with large predators. Firstly, the carcass portions to be consumed by the predators are very heterogeneous in terms of the macroscopic and nutrient composition. Secondly, large predators tend to eat different parts of the animal carcass in varying quantities. Thirdly, in some cases large predators tend to consume most or sometimes all the food leaving little or nothing to analyse. Furthermore, in those cases where a predator leaves a portion of the carcass, the refusals are seldom of the same composition as the carcass that has been fed to the predator.

To overcome these challenges a specific procedure was developed in this study to feed the predators part of a carcass and obtain representative samples from the carcass for analysis. The animal carcasses that were used as diets consisted of two symmetrical portions or cuts and were divided in different sections, *e.g.* the two front limbs or the two hind limbs originating from the same carcass. In cases where a hind limb was too large for a single predator to consume, as was the case with the leopard and cheetah, smaller symmetrical sections of the hind limbs were used. Because of the destructive nature of the feed consumption by carnivores, one limb or a smaller limb section was fed to the specific predator as trial diet and the other section was retained as a mirror image carcass portion for nutrient analysis in the laboratory. With this procedure it was assumed that the mirror image of the trial diet was for all practical purposes identical in nutrient composition to the one fed to the carnivore.

3.5.1 Preparation of trial diets (carcass portions)

See **Appendix 1** for a step-by-step guide for the preparation of the trial diets. A schematic presentation of the experimental procedures followed in executing the intake and digestibility trials, is presented in Figure 3.2.

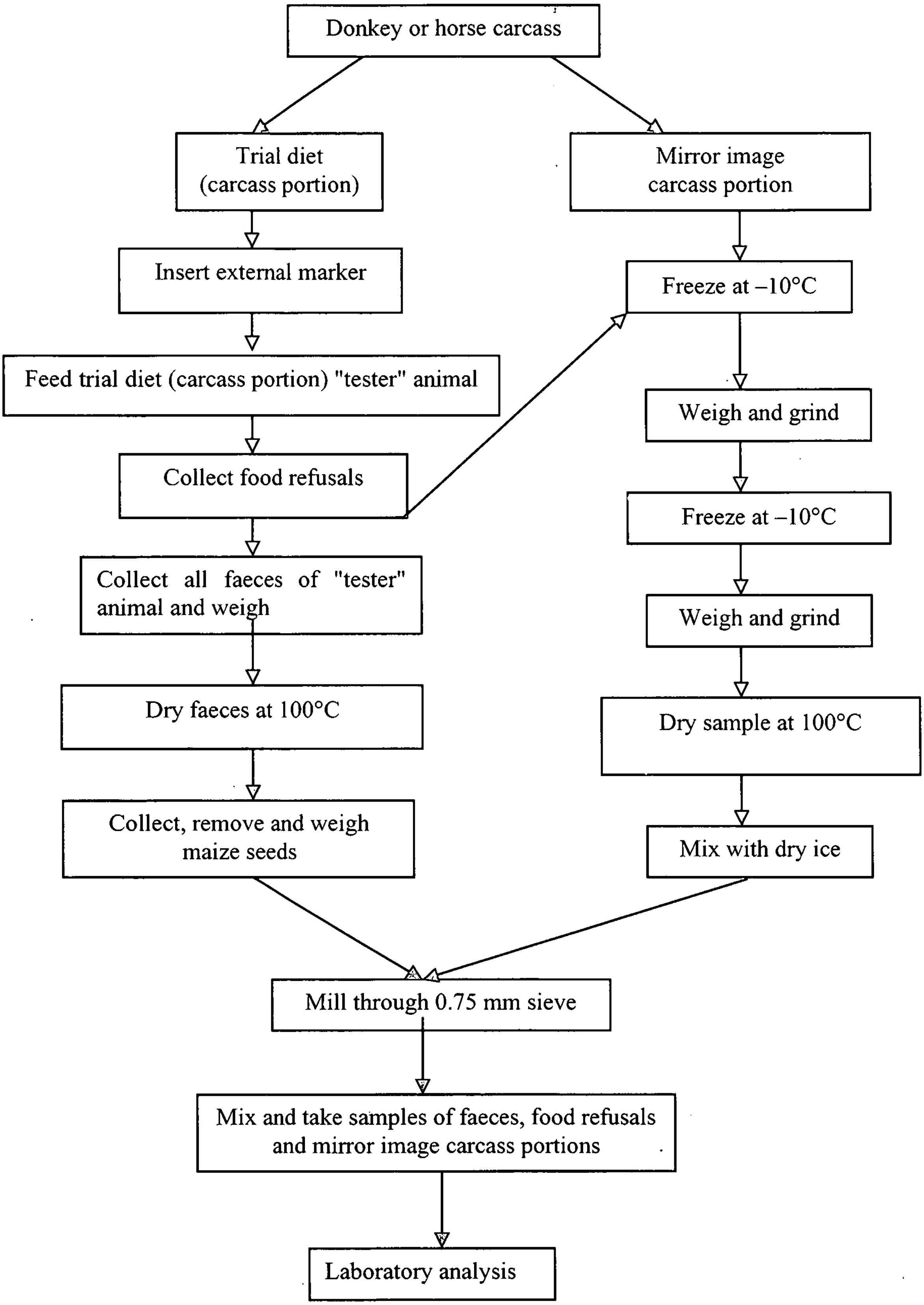

Figure 3.2 Schematic presentation of experimental procedures

3.5.1.1 Harvesting of horses and donkeys

The animals to be fed to the predators were humanely and instantly harvested by a single shot at a short distance to the forehead with a silenced rifle. Chasing and herding the donkeys was kept to an absolute minimum. The carcass was then immediately loaded on a flatbed utility vehicle, using a winch to assist in the loading process. Shortly thereafter the carcass was taken to the butchery facility at the Bloemfontein Zoo where it was eviscerated but not skinned.

3.5.1.2 Separation of fore and hind limbs from the carcasses

The fore limbs were separated from the carcass by using a large butcher's knife to cut alongside the ribcage. The lower part of the front leg was removed by using a commercial meat saw to cut and severe it just below the carpus. The hind limbs were separated from the carcass by cutting between the last lumbar and first sacral vertebrae. Using a commercial meat saw to cut through the length of the sacral vertebrae separated the two hind limbs (hindquarters). Another method to separate the hind limbs from the carcass is to simply cut through the joint between the femur and the pelvic bone (acetabulum). The lower part or the hind leg was removed by cutting through the joint just below the tibia above the tarsus.

The front and hind limbs that were fed are referred to as the "trial diet" and the symmetrical front and hind limbs that were analysed as the "mirror image carcass portion". Both the trial diets and mirror image carcass portions were weighed on a large Avery® platform scale, as well as visually inspected to ensure that they were of the same weight and shape. This was done to ensure that the two cuts resembled each other as closely as possible. The mirror image carcass portion was put into a large plastic bag, sealed and frozen pending laboratory analysis.

In the case of the lions, a whole hind limb of a donkey was fed at one feeding time. The leopards and cheetah were fed either a whole forelimb of a donkey or a smaller section (30 to 50%) of the hind limb of a horse.

Before feeding, the trial diet was weighed and the mass recorded. The approximate weights of the trial diets (carcass portions) were on a par with the amount of food the predators are accustomed to getting on feeding days in the Bloemfontein Zoo.

3.5.1.3 External marking of the trial diets (carcass portions)

The fact that a pair of predators shared the same leisure yard required the use of an external marker to identify each individual's faeces. It was a prerequisite that the marker should be easily identifiable in the faeces, safe for the predator to ingest and indigestible in the digestive tract of the carnivores. Another important criterion is that it should be possible to insert it into the trial diet without having to mince or mix the different sections of the carcass together. Several of these criteria made the use of known conventional external markers such as chromium oxide impractical or unsuitable.

Whole yellow maize seeds (*Zea mays*) complied with all three criteria mentioned above (Laurie Marker, 2001; personal communication) and maize is also cheap and easy to obtain.

Twenty whole maize seeds were inserted into each trial diet fed to the leopards and cheetah and 30 maize seeds were inserted into each trial diet fed to the lions. The maize seeds were distributed through the trial diet by punching holes through the skin and flesh using a knife and then inserting the maize seeds.

It must be noted that only the trial diet that was offered to the specific predator used in a trial (referred to as the "tester" predator or animal) was marked in this way. The other predator of the species that was not participating in the trial (referred to as the "filler" predator or animal) was fed either chicken tripe or a piece of ribcage of a donkey or horse of which the skin was removed. It was quite easy to distinguish between the faeces of the two animals with the dual system of identification.

3.5.1.4 Feeding of trial diets (carcass portions)

The trial diets were provided in accordance with the routine feeding program prescribed by the management of the Bloemfontein Zoo and to which the predators were accustomed. Before the animals were fed they were lured into the brick and concrete night chambers by opening the steel grate trapdoors (See figure 3.1). The predator taking part in the trial ("tester" predator) was lured into one of the sleeping chamber at the back of the night chamber (chamber B) and closed off with a steel grate trapdoor. The predator not taking part ("filler" predator) was then lured into the front chamber (chamber A) and also closed off. The large service gate leading to the leisure yard was then opened and the leisure yard inspected and cleaned of all pieces of food refusals, bone fragments and faeces from previous meals.

The “filler” animal’s food (ribcage or chicken tripe or whole chickens with the crops removed to prevent maize seeds ending up in the “filler” animal’s faeces) was then left in the leisure yard, the service gate closed and locked. The steel grate trapdoor leading from the night chambers to the leisure yard was then opened to let the “filler” animal out to start feeding without hindrance in the leisure yard. The steel grate trapdoor leading to the leisure yard was then closed again to prevent the “filler” animal from returning to chamber A.

The trial diet was then put into the front chamber (chamber A) by opening the chamber gate leading to the service area to the night chamber. After the gate was closed and locked, the ”tester” animal was allowed to feed on the trial diet that contained maize seeds as external markers. The time of the feeding was recorded. The “tester” animal was left overnight in the night chambers to allow ample time for it to consume as much of the trial diet as possible.

3.6 Collection of food refusals and faeces

3.6.1 Collection of food refusals

The food refusals of the trial diets were collected the next morning. The “tester” animal was lured into the back chamber (chamber B) and the steel grate door separating the two chambers closed. The parts of the trial diets that were not consumed by the predator (food refusals) were collected through the small service gate, put in plastic bags and sealed. The food refusals were taken to the laboratory and the weight recorded. The refusals were frozen and stored at -10°C pending further processing.

The “filler” predator was lured into the front night chamber (chamber A) and the steel grate trapdoor closed. The leisure yard was then cleaned of any food refusals and faeces of the “filler” predator.

The large service gate was then closed and both the “tester” and “filler” predators were allowed back into the leisure yard.

3.6.2 Collection of faeces

All marked faeces excreted by the "tester" predators were collected from early in the morning after the trial diet was consumed. The time of collection was recorded. Inspections for fresh faeces were made at three-hour intervals only during the daylight hours of the day to minimise the disturbance of the predators. The faeces were picked up from the ground by means of a large metal spatula and put into airtight plastic bags. The faeces were then weighed, frozen and stored with the food refusals. All visible contamination *e.g.* grasses, twigs and soil, were removed before weighing.

3.7 Identification of the faeces

During a trial only the "tester" predator’s faeces, originating from feeding on the trial diet, were collected. The visual presence of maize seeds in the faeces, as well as the presence of hair from the trial diets, identified the relevant animals’ faeces. The last faeces from a previous feeding could also be distinguished from the first faeces of the next feeding by the presence of hair and a firmer texture versus the softer, dark and fairly hair-free faeces marking the beginning of the next feeding’s defecation. The first faeces from a feeding are always darker in colour, soft in texture and hair-free while the last faeces of a feeding is always firmer and dryer. The last faeces also contain large quantities of hair if the animal was fed a diet containing hair.

The “filler” predator’s faeces were easily identified by a number of characteristics. The faeces originating from chicken diets were lighter or paler in colour and the faeces originating from the ribcage where large quantities of bone was consumed, usually had a crumb-like texture and a whitish colour. The presence of feathers and the unmistakable fragments of chicken and rib bone were also important in the identification of the faeces of the “filler” predator.

3.8 Laboratory processing of the mirror image carcass portions, food refusals and faeces

3.8.1 Processing of the mirror image carcass portions and food refusals

3.8.1.1 Grinding of the mirror image carcass portions and food refusals

The solid frozen mirror image carcass portions were taken from the freezer and cut into smaller pieces using a conventional, commercial meat saw (see Plate 1A) and then kept frozen again in the freezer. The frozen smaller pieces of carcass were then ground through a heavy duty, whole animal carcass grinder (see Plates 1B, C and D). The carcass grinder is equipped with 57 circular saw-toothed blades, each with a diameter of 300 mm. The blades are fitted next to each other with a 3 mm spacing on to a single axle propelled by two fan belts pulled by a 10 HP electric motor. The carcass pieces are kept in contact with the blades and forced through the grinder by a wooden block, propelled by slowly turning a manually operated screw plunger. The circular blades and meat is covered with a heavy steel lid, securely closed and held in place by a pair of large winged nuts and bolts to prevent pieces of the carcass being flung from the grinder. The ground carcass comprising meat, bone, skin and hair, soft and connective tissue were collected in a plastic meat crate. All the small pieces of ground carcass adhering to the meat saw and carcass grinder were collected using a metal scraper to clean the equipment. The scrapings were added to the ground carcass, making sure that only as little of the ground carcass as possible was lost. The ground carcass was quantitatively transferred into a plastic bag, sealed and refrozen. The process was then repeated, effectively grinding each carcass twice. After the second grinding, the ground carcass material was collected and transferred quantitatively to a commercial bowl processed meat mixer and mixed thoroughly. However, it should be noted that even after the second grinding procedure, the carcass material was still relatively coarse. After mixing, the ground carcass material was transferred to a plastic bag and weighed. A representative sample was taken, frozen and stored in a plastic bottle with screw-on lid pending further processing.

The food refusals comprising the parts of the trial diet that was not ingested by a specific animal, was processed in the same way as the mirror image carcass portions as described above.

Plate 1A

Plate 1B

Plate 1C

Plate 1D

Plate 1 Photographic presentations of the equipment used in the processing of the mirror image carcass portions and food refusals for laboratory analyses

It must be noted that the mirror image carcass portions and food refusals of each of the 16 trials were handled and processed separately.

3.8.1.2 Drying of carcass portions and food refusal samples

Two methods of drying the carcass portions and refusals were tested, namely drying in a force draught oven at 100°C versus freeze-drying. Both procedures were used to determine if the less cumbersome drying in a force draught oven could be used instead of freeze-drying. There was no significant difference ($P>0.05$) between the two drying methods in terms of the DM content of the carcass samples. However, the CP content of samples dried in a force draught oven at 100°C was significantly ($P\leq0.05$) higher than in samples that were freeze dried; an observation that could not be explained.

Based on the results of the testing of the drying methods, it was decided that all samples would be dried in the force draught oven.

The carcass portions and food refusal samples were weighed in duplicate onto pre-weighed stainless steel pans. The samples were dried in a force draught oven at 100°C for 16 hours and the DM content of the samples determined.

3.8.1.3 Calculation of a correction factor for water loss due to the grinding of carcass material and food refusals

Due to considerable heat produced by the friction of the grinder blades against the frozen carcass, containing flesh, bone, skin and hair, a significant ($P\leq0.05$) amount of water was lost during grinding in the form of visible water vapour or steam (see Plate 1C). The procedures for calculating factors to correct for the water loss of the carcass and food refusals are shown in Tables 3.3 and 3.4. as well as the loss of water due to friction caused by the grinding process. In Trial 1 replication 1 and 2 a mean correction factor derived from Trial 1 replication 3 and Trial 2 replication 1 to 3 was used for the carcass and food refusals respectively. The reason for this procedure was that the importance of the water loss in the form of visible water vapour or steam was not realised yet at that point in time and no correction for the water loss was made.

Recently, the fore and hind limbs and skin of donkeys were fed to lions in the Bloemfontein Zoo and the gross composition and DM content of the mirror image carcass portions of the respective carcass components determined by means of dissection in the laboratory (Yanna Smith & H.O. de Waal, 2001; personal communication). A comparison of those results with the results obtained in the first two trials of this study, pointed to the obvious loss of a substantial quantity of water during the grinding of the frozen carcass portions. This initiated a separate investigation, showing that about 200 g water/kg fresh carcass is lost due to the grinding of the frozen carcass components. Strangely, no reference to even the possibility of such a phenomenon could be found in literature.

The uncorrected DM content on each of the mirror image carcass portions and food refusals was then multiplied by the correction factors calculated for each trial replication to calculate the true or corrected DM content of the mirror image carcass portions and food refusals.

3.8.1.4 Milling of the ground and dried carcass and refusal samples

The dried ground carcass and food refusals samples were mixed in a ratio of 1:1 (volume: volume) with crushed dry ice 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. The small particle size of the final samples ensured a homogeneous composition for sub-sampling and nutrient analysis.

The milled carcass and food refusal samples were placed in plastic containers with screw-on lids and stored again at –10°C pending nutrient analysis.

Table 3.3 Calculation of the correction factors for water loss due to grinding of frozen carcass portions

Trial	Predator	Replication	Mass before grinding (g)	Mass after one grinding (g)	Water loss (g)	Water loss (g/kg)	Mass after two grindings + mixing (g)	Water loss (g)	Water loss (g/kg)	Total water loss (g)	Total water loss (g/kg)	Correction factor
			A	B	C = A - B	D = C/A*1000	D	E = B - D	F = E/B*1000	G = C + E	H = G/A*1000	I = 1 - (G/A)
1	Lion male	1	Not available									0.8074
		2	Not available									0.8074
		3	15825	13628	2197	138.83	12855	773	56.72	2970	187.68	0.8123
2	Lion female	1	15596	13443	2153	138.05	12578	865	64.35	3018	193.51	0.8065
		2	10957	8866	2091	190.84	8382	484	54.59	2575	235.01	0.7650
		3	14941	12247	2694	180.31	11560	687	56.10	687	56.10	0.9540
3	Leopard male	1	6583	5280	1303	197.93	5070	210	39.77	1513	229.83	0.7702
		2	5838	5074	764	130.87	4847	227	44.74	991	169.75	0.8303
		3	9228	6808	2420	262.25	6374	434	63.75	2854	309.28	0.6907
4	Leopard female	1	6948	4942	2006	288.72	4691	251	50.79	2257	324.84	0.6752
		2	6619	5771	848	128.12	5448	323	55.97	1171	176.91	0.8231
		3	5692	4304	1388	243.85	4089	215	49.95	1603	281.62	0.7184
5	Cheetah male	1	5103	4400	703	137.76	4090	310	70.45	1013	198.51	0.8015
		2	5774	4507	1267	219.43	4282	225	49.92	1492	258.40	0.7416
		3	7593	6282	1311	172.66	5997	285	45.37	1596	210.19	0.7898
6	Cheetah female	1	6520	6082	438	67.18	5907	175	28.77	613	94.02	0.9060

Table 3.4 Calculation of the correction factors for water loss due to grinding of food refusal samples

			Mass before grinding (g)	Mass after one grinding (g)	Water loss (g)	Water loss (g/kg)	Mass after two grindings + mixing (g)	Water loss (g)	Water loss (g/kg)	Total water loss (g)	Total water loss (g/kg)	Correction factor
Trial	Predator	Replication	A	B	C = A - B	D = C/A*1000	D	E = B - D	F = E/B*1000	G = C+E	H = G/A*1000	I = 1 – (G/A)
1	Lion male	1	Not available									0.6867
		2	Not available									0.6867
		3	1399	1036	363	25.95	971	65	6.27	428	30.59	0.6941
2	Lion female	1	893	674	219	24.52	637	37	5.49	256	28.67	0.7133
		2	1340	932	408	30.45	846	86	9.23	494	36.87	0.6313
		3	1519	1089	430	28.31	1003	86	7.90	516	33.97	0.6603
3	Leopard male	1	1276	931	345	27.04	880	51	5.48	396	31.03	0.6897
		2	1010	803	207	20.50	761	42	5.23	249	24.65	0.7535
		3	2063	1514	549	26.61	1438	76	5.02	625	30.30	0.6970
4	Leopard female	1	3249	2177	1072	32.99	2090	87	4.00	1159	35.67	0.6433
		2	3036	2351	685	22.56	2246	105	4.47	790	26.02	0.7398
		3	3124	2427	697	22.31	2193	234	9.64	931	29.80	0.7020
5	Cheetah male	1	290	179	111	38.28	179	0	0.00	111	38.28	0.6172
		2	744	538	206	27.69	538	0	0.00	206	27.69	0.7231
		3	716	588	128	17.88	555	33	5.61	161	22.49	0.7751
6	Cheetah female	1	1373	1140	233	16.97	1080	60	5.26	293	21.34	0.7866

3.8.2 Processing of faeces

Each collection of faeces of a trial was individually dried on stainless steel trays in a force draught oven at 100°C for 16 hours and the DM content determined. The maize seeds were removed and weighed. The weight of the maize was subtracted from the dry mass of the faeces.

After drying in the oven the faeces were milled through a 0.75 mm screen in a conventional Wiley mill and mixed. Representative samples were placed into plastic containers with screw-on lids and stored pending nutrient analysis.

3.9.1 Laboratory analysis of mirror image carcass portions, refusals and faeces

3.9.1 Crude protein (CP)

The CP content of the mirror image carcass portions, refusals and faeces was determined on a DM basis with a Leco ® nitrogen (N) analyser (Leco® Corporation, 2001). A factor of 6.25 was used to convert the N content of samples to CP content.

3.9.2 Lipids

The lipid content of the mirror image carcass portions, refusals and faeces was determined in a soxhlet apparatus by using the hexane method (AOAC, 2000).

The high lipid content of the carcass portion and refusal samples caused smearing of fat onto the glass apparatus. Therefore, the lipid content of the carcass portions and refusal samples was determined by extracting the lipid from samples directly from the sample bottles. Another sample was taken from the sample bottles and dried overnight to correct for any moisture gain while in the bottle. All lipid analysis was done in triplicate.

3.9.3 Minerals (ash)

The mineral (ash) content of the mirror image carcass portions, refusals and faeces was determined on a DM basis by ashing the samples in duplicate in porcelain crucibles for four hours in a muffle furnace at 600°C (AOAC, 2000).

3.9.4 Gross energy (GE)

The gross energy (GE) of the mirror image carcass portions, refusals and faeces was determined on a DM basis by using an adiabatic bomb calorie meter (AOAC, 2000).

3.10 Calculation of the nutrient composition of food intake

The nutrient composition of the trial diets fed to each "tester" predator was calculated by multiplying the DM, CP, lipid, and mineral content of the mirror image carcass portion samples (expressed in g per kg) with the mass (kg) of the trial diets fed to the "tester animals". The nutrient composition of the food refusals was calculated in a similar way by multiplying the nutrient composition of the food refusals by the total mass of the food refusals retrieved from each trial.

The nutrient composition of the actual food and nutrient intake of the "tester" predator in each trial was determined by subtracting the total quantity (expressed in kg) of DM, CP, lipid, minerals and GE in the refusals from that in the mirror image carcass portions.

A summary of the nutrient composition of the donkey and horse carcass portions fed to the predators is shown in Table 3.5.

3.11 Calculation of apparent digestibility coefficients of food and nutrients

According to McDonald *et al.* (1995) the apparent digestibility of food or nutrients is best defined as the proportion of food or nutrients not excreted in the faeces and therefore assumed to be absorbed by the animal.

The following formula is used to calculate apparent digestibility coefficients:

$$\text{Apparent digestibility coefficient} = \frac{\text{(food or nutrient intake) - (food or nutrient excreted in faeces)}}{\text{Food or nutrient intake}}$$

where Intake (kg) = kg food or nutrient presented – kg food or nutrient refused

Table 3.5 Summary of the nutrient composition of the donkey and horse carcass portions fed in this study to African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

Trial	Predator	Replication	Dry matter (DM) (g/kg)	Crude protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (Ash) (g/kg DM)	Gross energy (GE) (MJ/kg DM)
1	Lion male	1	380	609	222	171	22.720
		2	347	621	165	199	22.209
		3	337	577	271	142	25.184
2	Lion female	1	295	655	184	156	23.778
		2	339	617	180	181	22.215
		3	445	539	288	143	24.145
3	Leopard male	1	356	575	216	185	21.971
		2	356	575	216	185	21.971
		3	341	632	173	183	21.406
4	Leopard female	1	385	497	213	270	19.187
		2	284	700	152	136	22.620
		3	394	555	210	202	22.507
5	Cheetah male	1	275	718	121	142	22.953
		2	320	636	170	188	21.506
		3	285	767	100	138	21.409
6	Cheetah female	1	392	526	267	176	24.432
	Mean		345.8	612.3	196.8	174.9	22.5
	SD		47.0	72.7	51.8	34.0	1.4
	CV		13.6	11.9	26.3	19.4	6.4

3.12 Statistical analysis

The data was statistically analysed using GLM procedures of SAS (1991).

4 Results and Discussion

The results on food intake and digestibility of the African lions, leopards and cheetah are presented and discussed in separate sections, starting with the lion.

4.1 Intake and digestibility studies with African lions (*Panthera leo*)

Most studies assume that lions are able to extract sufficient and balanced quantities of nutrients from their diets. According to Smuts (1978) lions have a feeding interval of four days in the Kruger National Park and it was found that 50% of the lion stomachs examined were empty, therefore, a complete digestion time of two days by lions was assumed.

4.1.1 Food intake and apparent digestibility

The fresh food intake, fresh faecal excretion and thus apparent digestibility of fresh food is shown in Table 4.1.1.

Table 4.1.1 Fresh food intake, faecal excretion and the apparent digestibility of fresh diets consisting of donkey carcass portions (on a fresh, or as fed, basis) by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient	Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient
1	15.069	1.686	0.888	1	14.703	1.604	0.891
2	10.881	1.222	0.888	2	10.054	0.643	0.936
3	14.580	1.588	0.891	3	13.681	0.565	0.959
Mean	13.510	1.499	0.889	Mean	12.812	0.938	0.929
SD	2.290	0.245	0.002	SD	2.443	0.579	0.035
CV	16.950	16.327	0.208	CV	19.069	61.723	3.717

The mean food intake on a fresh (or as fed) basis was 13.5 kg and 12.8 kg for the male and female lion respectively. This implies an intake of 7.2% and 9.9% of the body weight of the male and female lion respectively. The voluntary food intake obtained was in accordance with estimated intake of food of lions in the wild of between 4.7 and 14 kg per day (Schaller, 1969; Eloff, 1973; Clark, 1987; Packer *et al.*, 1990; Stander, 1992; Mills & Biggs, 1993).

During all six trial replications conducted with the male and female lions, nearly all animal material of the trial diets were consumed. All that remained was the large bones and some connective tissue that could not be removed by the incisors of the lions. In some cases the epiphyses of the bones were eaten. One could assume that if larger carcass portions were presented to the lions, the food intake could have been higher. However, it was not an objective of this study to determine how much food lions could ingest. This is an important aspect that will be incorporated into the next phase of the research programme of ALPRU.

The mean apparent digestibility coefficients of the diets on a fresh (or as fed) basis were 0.889 and 0.929 for the male and female lions respectively.

The DM intake, faecal excretion and apparent digestibility of diets consisting of donkey carcass portions by the male and female lions are shown in Table 4.1.2.

Mean apparent DM digestibilities of 0.854 and 0.902 for the male and female lions respectively were obtained. This is in close accordance with the apparent digestibility coefficient of 0.869 obtained with a sub-adult male using a hindquarter of a Red Hartebeest (*Alcelaphus buselaphus*) cow by Yanna Smith & H.O de Waal (2000, personal communication). However, the DM digestibility coefficients obtained in this study is substantially higher than those reported in literature, for example, Morris *et al.* (1974) and Barbiers *et al.* (1982) obtained DM digestibility coefficients of 0.760 and 0.757 respectively using a minced meat-based commercial diet. Interestingly, a mean apparent DM digestibility coefficient of 0.946 was obtained with domestic cats (*Felis catus*) when minced meat was used as diet (Kendall *et al.*, 1982).

Table 4.1.2 Dry matter (DM) intake, faecal excretion and the apparent DM digestibility of diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient	Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient
1	5.396	0.684	0.873	1	4.068	0.672	0.835
2	3.560	0.556	0.844	2	3.074	0.274	0.911
3	4.522	0.702	0.845	3	5.829	0.230	0.961
Mean	4.493	0.647	0.854	Mean	4.324	0.392	0.902
SD	0.919	0.079	0.017	SD	1.395	0.244	0.063
CV	20.448	12.270	1.964	CV	32.264	62.202	7.029

Although the coefficients of variation were fairly low in both cases, higher coefficients of variation of the DM intake (see Table 4.1.2) compared to that of the fresh food intake (Table 4.1.1) were obtained. This is the result of the variation in the trial diets' composition in terms of water content. This is the reason why it is preferred to express intake in terms of DM intake rather than as fresh food (as fed) intake or intake in terms of percentage of body mass of a particular animal. Furthermore, the expression of food intake by large predators as a percentage of body mass is not feasible because this would entail the regular weighing of the predator. Indeed, the procedure of weighing these animals is a difficult and in some cases dangerous activity (see 3.4).

The low coefficients of variation found in these cases for the apparent digestibilities of fresh and DM in food (Tables 4.1.1 and 4.1.2) suggest that there was a high measure of repeatability in the techniques that were applied.

4.1.2. Nutrient intake and apparent digestibility

The composition of the food ingested by a male and female lion is shown in Table 4.1.3.

Table 4.1.3 Composition of the food intake from diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial	Predator	Replication	Dry matter (DM) (g/kg0	Crude Protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (g/kg DM)	Gross energy (GE) (MJ/kg DM)
1	Male lion	1	358.105	648.877	240.744	123.801	24.032
		2	327.151	655.845	177.704	157.676	23.477
		3	310.163	630.336	299.336	77.894	27.242
2	Female lion	1	276.709	700.458	193.343	115.676	24.935
		2	305.765	707.755	173.057	108.357	23.998
		3	426.046	579.409	289.580	91.823	25.385
	Mean		333.990	653.780	228.961	112.538	24.845
	SD		52.437	47.331	56.192	27.644	1.364
	CV		15.700	7.240	24.542	24.564	5.488

4.1.2.1 Crude protein (CP) intake and apparent digestibility

The CP intake and faecal excretion and the apparent CP digestibility of the diets by a male and female lion are shown in Table 4.1.4.

The very high apparent CP digestibility coefficients show the extent to which the most important nutrient of the carnivorous diet, CP, is digested by lions. Barbiers *et al.* (1982) using a commercial minced meat-based diet, and Morris *et al.* (1974), using a venison- based diet, respectively, obtained apparent CP digestibility coefficients of 0.831 and 0.888 with lions. In a study with domestic cats (*Felis catus*) the mean apparent CP digestibility coefficient was 0.981 (Kendall *et al.*, 1982).

Table 4.1.4 Crude protein (CP) intake, faecal excretion and apparent CP digestibility of diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Trial	Crude protein (CP) intake (kg)	Crude protein (CP) excreted (kg)	Digestibility coefficient	Trial	Crude protein (CP) intake (kg)	Crude protein (CP) excreted (kg)	Digestibility coefficient
1	3.502	0.240	0.931	4	2.850	0.236	0.917
2	2.335	0.179	0.923	5	2.176	0.112	0.949
3	2.850	0.284	0.900	6	3.377	0.087	0.974
Mean	2.996	0.234	0.919	Mean	2.801	0.145	0.947
SD	0.585	0.053	0.016	SD	0.602	0.080	0.029
CV	20.196	22.581	1.750	CV	21.503	55.264	3.030

4.1.2.2 Lipid intake and apparent digestibility

Sinclair (1975) as cited by Davidson *et al.* (1986) stated that two species of Carnivora, the domestic cat (*Felis catus*) and the African lion (*Panthera leo*) lack the ability to further desaturate the essential fatty acids polyenoic, linoleic (*cis*-C18: 2ω) and α-linolenic (*cis*-C18: 3ω3), due to an apparent absence of the active form of the enzyme Δ-6-desaturase. This results in carnivores having specific dietary requirements for animal fat. The need for a dietary supply of these fatty acids arises from the inability of mammals to introduce double bonds between the ninth carbon atom and the terminal methyl group of the fatty acid chain (McDonald *et al.*, 1995).

The lipid intake, faecal excretion and apparent lipid digestibility coefficients for a male and female lion are shown in Table 4.1.5.

Lipids are also digested to a very large extent by lions. This is especially important since lipids have a higher energy content than protein (McDonald *et al.,* 1995). Barbiers *et al.* (1982) reported a lipid digestibility coefficient of 0.947 for lions using a commercial meat-based diet, while Kendall *et al.* (1982) reported an apparent lipid digestibility coefficient of 0.957 for domestic cats.

Table 4.1.5 Lipid intake, faecal excretion and apparent lipid digestibility of diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient	Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient
1	1.299	0.006	0.996	1	0.787	0.008	0.990
2	0.633	0.004	0.994	2	0.532	0.005	0.991
3	1.354	0.005	0.996	3	1.688	0.004	0.997
Mean	1.095	0.005	0.995	Mean	1.002	0.006	0.993
SD	0.402	0.001	0.001	SD	0.607	0.002	0.004
CV	36.663	20.189	0.108	CV	60.605	32.428	0.404

4.1.2.3 Intake and apparent digestibility of minerals (ash)

The apparent digestibility of the ash fraction is an indication of how well the predator can digest minerals. The mineral intake, faecal excretion and apparent mineral digestibility for a male and female lion are shown in Table 4.1.6.

The apparent digestibility of minerals in Trial 1, replication 3 was corrected to zero due to the retention of possibly a piece of bone in the digestive tract from a previous feeding. Although lions are feast and famine feeders, this does not mean that the gastro-intestinal tract is completely cleared of all indigestible animal matter after a feeding. Blackened bones have been retrieved from the stomachs of lion carcasses, suggesting that larger pieces of bone might be trapped for a considerable time in the stomach before it passes down the intestines and is excreted (H.O. de Waal, 2002, personal communication).

Table 4.1.6 Mineral intake, faecal excretion and apparent mineral digestibility of diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient	Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient
1	0.668	0.336	0.498	1	0.471	0.367	0.220
2	0.561	0.319	0.431	2	0.333	0.147	0.559
3	0.352	0.353	0.000*	3	0.535	0.105	0.804
Mean	0.527	0.336	0.310	Mean	0.446	0.206	0.528
SD	0.161	0.017	0.270	SD	0.103	0.141	0.294
CV	30.471	5.042	87.262	CV	23.130	68.319	55.623

* Corrected to zero (see section 4.1.2.3)

4.1.2.4 Gross energy (GE) intake and apparent digestibility

The GE intake, faecal excretion and apparent GE digestibility coefficients of diets by a male and female lion are shown in Table 4.1.7.

Barbiers *et al.* (1982) reported apparent GE digestibilities of 0.861 by lions using a commercial meat-based diet and Kendall *et al.* (1982) reported a GE digestibility coefficient of 0.950 by domestic cats.

Table 4.1.7 Gross energy (GE) intake, faecal excretion and apparent GE digestibility of diets consisting of donkey carcass portions by a male and female African lion (*Panthera leo*)

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Gross energy (GE) intake (MJ)	Gross energy (GE) excreted (MJ)	Digestibility coefficient	Replication	Gross energy intake (GE) (MJ)	Gross energy excreted (GE) (MJ)	Digestibility coefficient
1	129.682	9.970	0.923	1	101.444	8.293	0.918
2	83.570	5.448	0.935	2	73.770	4.883	0.934
3	123.195	8.282	0.933	3	147.960	4.520	0.969
Mean	112.149	7.900	0.930	Mean	107.725	5.898	0.941
SD	24.962	2.285	0.006	SD	37.491	2.082	0.026
CV	22.258	28.928	0.672	CV	34.803	35.291	2.791

4.1.3 Excretion of faeces

Food passes quickly through the digestive system of lions and lions are capable of eating a meal relatively quickly by gorging themselves (Skinner & Smithers, 1990).

The faeces of lions are usually rough in texture and besides the remains from digested meat, it contains large amounts of hair and in some instances sand, seeds, leaves, feathers, grass and even porcupine quills (Eloff, 1999). The time intervals and faecal mass excreted by a male and female lion are shown in Figure 4.1.1.

Throughout the study it was noted that the lions did not have a latrine or a favourite place where they defecated in the leisure yard. The selection or choice of a suitable place to defecate seemed to be at random.

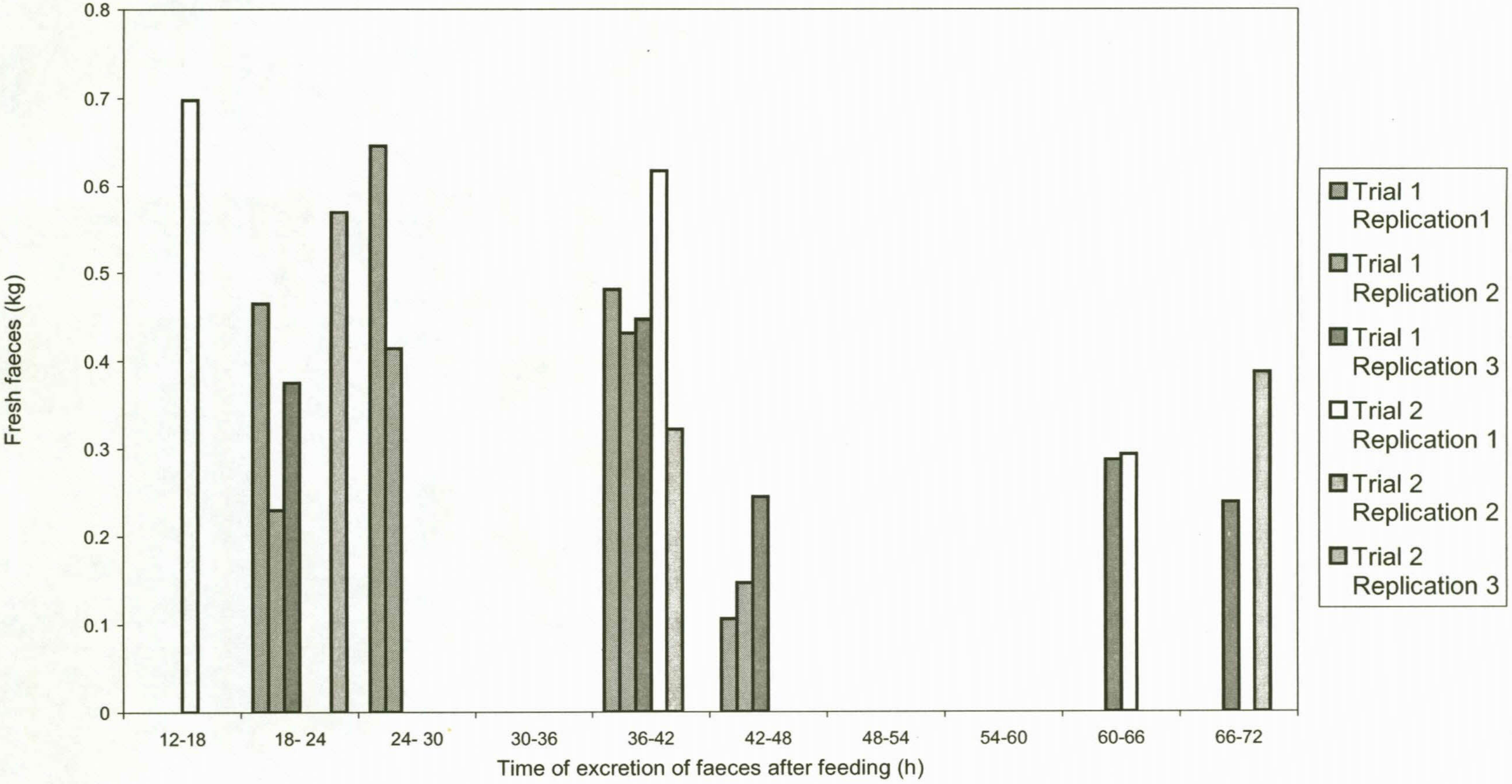

Figure 4.1.1 Fresh faeces (kg) excreted relative to feeding by a male (Trial 1) and female (Trial 2) African lion (*Panthera leo*)

The consistency of the faecal matter changed throughout the period after feedings. The first faeces or scat has a lower DM content than that excreted last. The first scat was also darker in colour than the last collection. The dark colouration of the first scat is presumably due to the higher contents of blood pigmentation relative to later scats. The shape of the scat also starts out as soft and pasty in texture changing to a harder and "sausage" or cylindrical shape. The last scat also contained more hair and grass. The last scat excreted after a feeding has a greater DM content and is sometimes completely comprised out of hair. The practical implication of these observations regarding the shape and consistency of scat is that when fresh scat is collected, the sequence of the scats relative to each other can be determined by means of a visual assessment of the DM content and shape of the different scats.

The increase in DM content of faeces is described by the following linear regression equations:

$y = 22.199X + 369.11$

$R^2 = 0.5671$ for the male lion

and

$y = 27.581X + 359.05$

$R^2 = 0.9375$ for the female lion.

The regression lines of the mean increase in DM in later defecations are shown in Figure 4.1.2.

The progressively higher DM content of the scat also suggests that the longer retention in the gastro-intestinal tract allows for greater absorption of water from the gut.

The composition of the faeces excreted by a male and female lion is shown in Table 4.1.8.

Table 4.1.8 Composition of faeces collected from a male and female African lion (*Panthera leo*)

Trial	Predator	Replication	Dry matter (DM) (g/kg)	Crude protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (g/kg DM)	Gross energy (GE) (MJ/kg DM)
1	Lion male	1	405.385	351.700	8.111	490.889	14.585
		2	455.096	321.200	6.656	573.911	9.796
		3	441.957	404.500	7.318	502.962	11.799
2	Lion female	1	419.196	351.400	11.439	546.040	12.332
		2	425.773	408.800	17.771	536.260	17.827
		3	406.578	377.000	18.665	456.058	19.671
	Mean		425.664	369.100	11.660	517.687	14.335
	SD		19.744	34.065	5.347	42.528	3.789
	CV		4.638	9.229	45.857	8.215	26.430

The mean faecal CP content of 425.664 g/kg shows the extent to which indigestible hair originating from the carcass portion passes through the digestive system. The low mean faecal lipid content of 11.660 g/kg shows the large extent to which lipids are digested and absorbed in the digestive tract. The faecal mineral content is largely due to the pieces of indigestible bone passing through the digestive tract. The low mean faecal GE content of 14.335 MJ/kg shows the large extent to which GE is extracted from the diet.

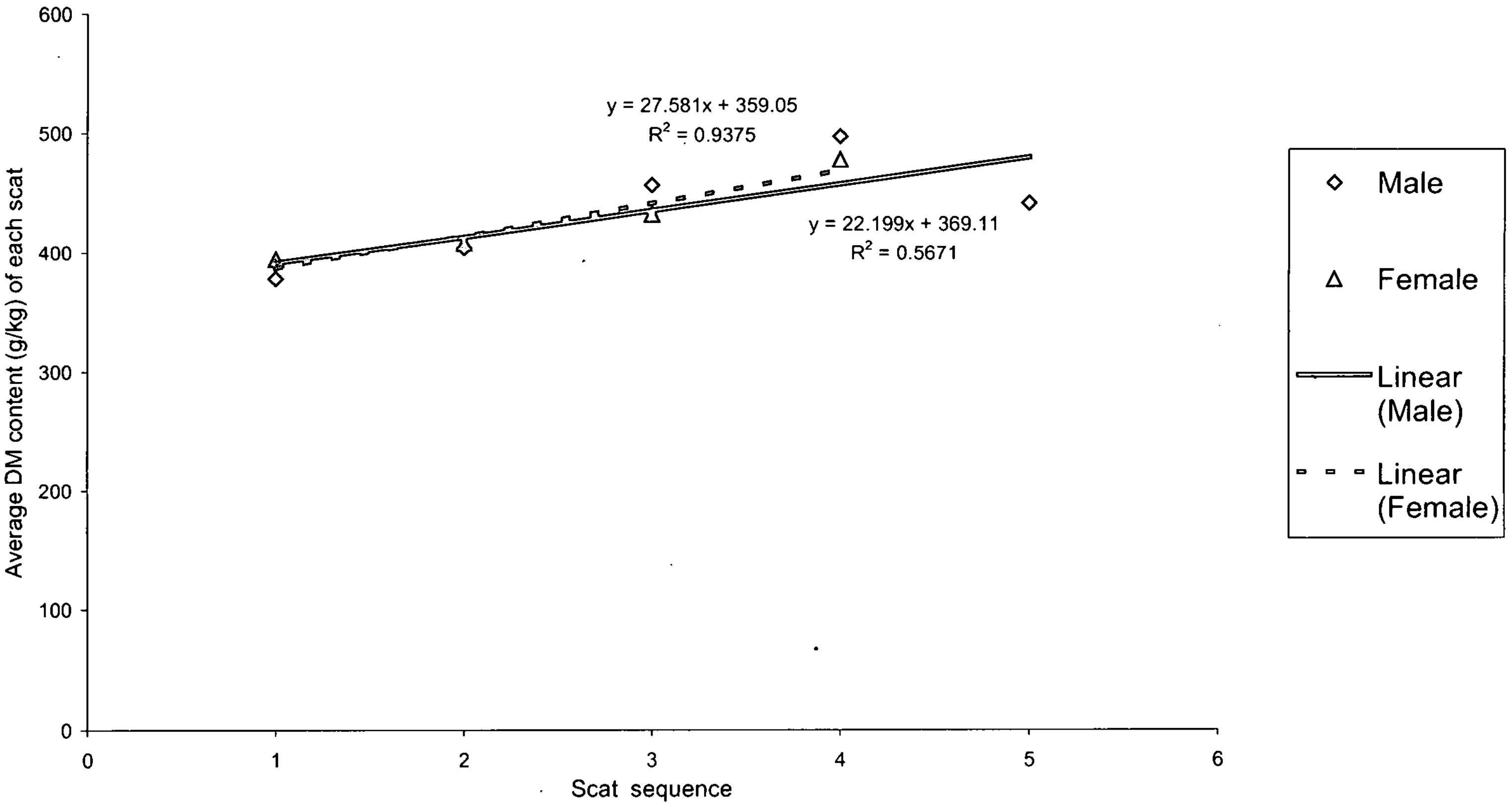

Figure 4.1.2 Regression line of faecal DM content (g/kg) for successive scats excreted by a male and female African lion (*Panthera leo*) after feeding

4.2 Intake and digestibility studies with leopard (*Panthera pardus*)

Except for experiments conducted by Morris *et al.* (1974) and Barbiers *et al.* (1982) where minced meat-based commercial diets and minced venison have been fed to leopards and other wild felidae, little quantitative information is available on the digestive efficiencies of leopards.

4.2.1 Food intake and apparent digestibility

Very little information is available on the actual food intake of leopards in the wild. Therefore, the basic experimental procedures for feeding and scat collections were similar to those used for the lions in this study. The food intake, faecal excretion and apparent digestibility of the trial diets on a fresh (or as fed) basis by the leopards are shown in Table 4.2.1.

Table 4.2.1 Fresh food intake, faecal excretion and the apparent digestibility of fresh diets consisting of donkey or horse carcass portions (on a fresh, or an as fed, basis) by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient	Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient
1*	5.200	0.314	0.940	1*	3.951	0.126	0.968
2*	4.946	0.262	0.947	2**	3.464	0.084	0.976
3*	6.926	0.349	0.950	3**	3.076	0.182	0.941
Mean	5.691	0.308	0.945	Mean	3.497	0.131	0.962
SD	1.077	0.044	0.005	SD	0.438	0.049	0.018
CV	18.933	14.210	0.546	CV	12.537	37.866	1.918

* Donkey carcass portion

** Horse carcass portion

The unavailability of sufficient stock of donkey carcasses forced the ALPRU research team to use a horse carcass for some of the trials with the leopard female and cheetah male.

In all three trials with the male leopard as "tester", the whole carcass portions fed to the animal as the trial diets were consumed. Only the large bones were left uneaten. The female leopard however had a tendency to leave some of the trial diets as refusals. The female leopard ate most of the meat underneath the skin leaving most of the skin and hair uneaten. The mean fresh food intake per feeding was 5.691 kg and 3.497 kg for the male and female respectively. The mean fresh food intake per feeding comprised 10.7% and 10% of the body weight of the male and female respectively.

In Namibia it has been documented that females with cubs eat 2.5 kg, females eat 1.6 kg and males 3.3 kg of meat per day (Bothma & Walker, 1999). Before feeding, the leopard usually uses its incisors to remove the hair or fur of the prey animal and leave it in a neat pile (Bothma & Walker, 1999). This phenomenon was not observed during the trials with the male leopard and only observed once with the female leopard.

The food intake, faecal excretion and apparent digestibilities of the trial diet by a male and female leopard on a DM (DM) basis are shown in Table 4.2.2. Morris *et al.* (1974) using a venison-based diet and Barbiers *et al.* (1982) respectively reported apparent DM digestibility coefficients of 0.782 and 0.799 by leopards, using a minced meat-based commercial diet and chromium oxide as external marker.

As was the case with the lions (Tables 4.1.1 and 4.1.2) the apparent digestibilities of fresh food (Table 4.2.1) were again somewhat higher than the apparent digestibilities on a DM basis (Table 4.2.2).

Table 4.2.2 Dry matter (DM) intake, faecal excretion and the apparent DM digestibility of diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient	Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient
1*	1.495	0.118	0.921	1*	1.305	0.044	0.966
2*	1.418	0.097	0.932	2**	0.812	0.026	0.968
3*	1.929	0.179	0.907	3**	0.793	0.050	0.937
Mean	1.614	0.131	0.920	Mean	0.970	0.040	0.957
SD	0.275	0.043	0.012	SD	0.290	0.013	0.017
CV	17.056	32.657	1.350	CV	29.935	31.602	1.818

* Donkey carcass portion
** Horse carcass portion

The low coefficients of variation found in these trials for the apparent digestibilities of fresh and DM in food (Tables 4.2.1 and 4.2.2) suggest that there was a high measure of repeatability in the techniques applied.

4.2.2 Nutrient intake and apparent digestibility

The composition of the food ingested by a male and female leopard is shown in Table 4.2.3.

Table 4.2.3 Composition of the food intake from diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial	Predator	Replication	Dry matter (DM) g/kg DM	Crude protein (CP) g/kg DM	Lipid g/kg DM	Mineral g/kg DM	Gross energy (GE) MJ/kg DM
1	Leopard male	1	287.437	719.410	234.955	54.296	24.956
		2	286.777	712.956	227.101	88.845	23.781
		3	278.471	791.207	159.599	68.744	23.836
2	Leopard female	1	330.324	443.162	203.851	326.497	16.859
		2	234.486	800.429	124.855	71.026	23.413
		3	257.693	867.377	147.888	47.567	26.588
	Mean		279.198	722.423	183.041	109.496	23.239
	SD		32.253	148.266	45.255	107.274	3.333
	CV		11.552	20.523	24.724	97.971	14.342

4.2.2.1 Crude protein (CP) intake and apparent digestibility

The CP intake, faecal excretion and apparent CP digestibility coefficients for a male and female leopard are shown in Table 4.2.4.

Barbiers *et al*. (1982) obtained apparent CP digestibility coefficient of 0.873 by leopards using a meat-based commercial diet and Morris *et al*. (1974) using a venison-based obtained an apparent CP digestibility coefficient of 0.889 by leopards. The apparent CP digestibility coefficients observed in this trial are relatively higher both for the male (0.937) and female (0.973) leopards, but within reasonable limits from figures reported by Barbiers *et al*. (1982) and Morris *et al*. (1974).

Table 4.2.4 Crude protein (CP) intake, faecal excretion and apparent CP digestibilities of diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Crude protein (CP) intake (kg)	Crude protein (CP) excreted (kg)	Digestibility coefficient	Replication	Crude protein (CP) intake (kg)	Crude protein (CP) excreted (kg)	Digestibility coefficient
1*	1.075	0.064	0.940	1*	0.578	0.024	0.958
2*	1.011	0.051	0.950	2**	0.650	0.009	0.985
3*	1.526	0.121	0.921	3**	0.688	0.017	0.975
Mean	1.204	0.079	0.937	Mean	0.639	0.017	0.973
SD	0.281	0.037	0.015	SD	0.055	0.007	0.014
CV	23.298	47.383	1.578	CV	8.686	42.959	1.397

* Donkey carcass portion
** Horse carcass portion

4.2.2.2 Lipid intake and apparent digestibility

The lipid intake, faecal excretion and apparent lipid digestibility coefficients for a male and female leopard are shown in Table 4.2.5. Barbiers *et al.* (1982) reported a mean lipid digestibility coefficient of 0.972 for leopards using a minced meat-based diet.

Table 4.2.5 Lipid intake, faecal excretion and apparent lipid digestibility of diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient	Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient
1*	0.351	0.004	0.988	1*	0.266	0.000	0.998
2*	0.322	0.001	0.997	2**	0.101	0.001	0.991
3*	0.308	0.002	0.995	3**	0.117	0.002	0.986
Mean	0.327	0.002	0.993	Mean	0.162	0.001	0.992
SD	0.022	0.002	0.005	SD	0.091	0.001	0.006
CV	6.756	78.108	0.473	CV	56.220	55.843	0.603

* Donkey carcass portion
** Horse carcass portion

The apparent lipid digestibility coefficient observed in this trial are relatively in line with values reported by Barbiers *et al.* (1982) for both the male (0.993) and female (0.992) leopards.

4.2.2.3 Intake and apparent digestibility of minerals (ash)

The mineral intake, faecal excretion and apparent mineral digestibility for a male and female leopard are shown in Table 4.2.6.

These apparent digestibility coefficients for minerals are high when compared to the lions, considering that both the male and female leopards are adults and do not have a high mineral requirement, *e.g.* calcium and phosphorus for bone growth. However, a situation similar to lions (discussed under section 4.1.2.3) may have occurred namely that large bone fragments ingested might have been retained longer in the gastro-intestinal tract. However, one would not expect such a scenario during every meal presented to the leopards.

Table 4.2.6 Mineral intake, faecal excretion and apparent mineral digestibility of diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient	Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient
1*	0.081	0.033	0.591	1*	0.426	0.013	0.970
2*	0.126	0.037	0.704	2**	0.058	0.010	0.834
3*	0.133	0.058	0.561	3**	0.038	0.014	0.630
Mean	0.113	0.043	0.619	Mean	0.174	0.012	0.811
SD	0.028	0.013	0.075	SD	0.219	0.002	0.171
CV	24.716	31.253	12.157	CV	125.812	18.737	21.043

* Donkey carcass portion
** Horse carcass portion

4.2.2.4 Gross energy (GE) intake and apparent digestibility

The GE intake, faecal excretion and apparent GE digestibility coefficients of diets by a male and female leopard are shown in Table 4.2.7. Barbiers *et al.* (1982) reported apparent a GE digestibility of 0.891 for leopards using a meat-based commercial diet.

Table 4.2.7 Gross energy (GE) intake, faecal excretion and apparent GE digestibility of diets consisting of donkey or horse carcass portions by a male and female leopard (*Panthera pardus*)

Trial 3				Trial 4			
Male leopard				Female leopard			
Replication	Gross energy (GE) intake (MJ)	Gross energy (GE) excreted (MJ)	Digestibility coefficient	Replication	Gross energy (GE) intake (MJ)	Gross energy (GE) excreted (MJ)	Digestibility coefficient
1*	37.300	2.752	0.926	1*	22.003	0.833	0.962
2*	33.731	1.587	0.953	2**	19.017	0.389	0.980
3*	45.973	2.915	0.937	3**	21.075	0.960	0.954
Mean	39.001	2.418	0.939	Mean	20.699	0.727	0.965
SD	6.296	0.724	0.013	SD	1.528	0.300	0.013
CV	16.143	29.949	1.435	CV	7.384	41.175	1.330

*Donkey carcass portion
**Horse carcass portion

The apparent GE digestibility coefficients observed in this trial are relatively higher with figures reported by Barbiers *et al.* (1982) for both the male (0.939) and female (0.965) leopards.

4.2.3 Excretion of faeces

Field data on the aspects of food passage, digestion and defecation by leopards is scarce. In the southern Kalahari it has been documented that most of the undigested food of leopards appears in the faeces on the first day after ingestion, leopards have also been noticed to defecate only five days after ingestion of food (Bothma, 1997). Furthermore, according to Bothma (1997) the food retention time does not differ according to the prey species consumed. When leopards feed on a large prey for a number of days, they may defecate close to the carcass. However, it is not clear whether the contents of the faeces of a particular dropping are from the previous ingested meal.

According to Bothma & Le Riche (1994) the mean interval between defecation is 0.6 days for leopard males and 1.2 days for females in the southern Kalahari. The reason for the significant difference is not known. This is in contradiction to the belief that because of the smaller body size of the female a higher metabolic rate and thus rate of passage is assumed. The distances travelled between defecations vary quite considerably. Males travel a mean of 12.4 km and females 21 km between defecations. Again it is also not certain if the faeces of a particular defecation comprise the undigested material of the last feeding. The higher frequency of defecation by male leopards as well as the shorter distances travelled between defecations by male leopards may be as a result of the territoriality of leopard males and the activity of defecating in the process of marking their territory.

The time intervals and faecal mass excreted by a male and female leopard are shown in Figure 4.2.1.

Leopards are territorial animals in that both the male and the female defend their territories (Skinner & Smithers, 1990). On one occasion during this study it was found that the male leopard has defecated on top of one of the female's previous excrements. The excrements were clearly distinguishable by the different colour of the faeces originating from the trial diet fed to the leopard male "tester" and the chicken tripe fed to the leopard female "filler". It was also noted that the faeces were deposited on the walking trails in the leisure yard, perhaps a further indication that these animals mark their territories with faeces.

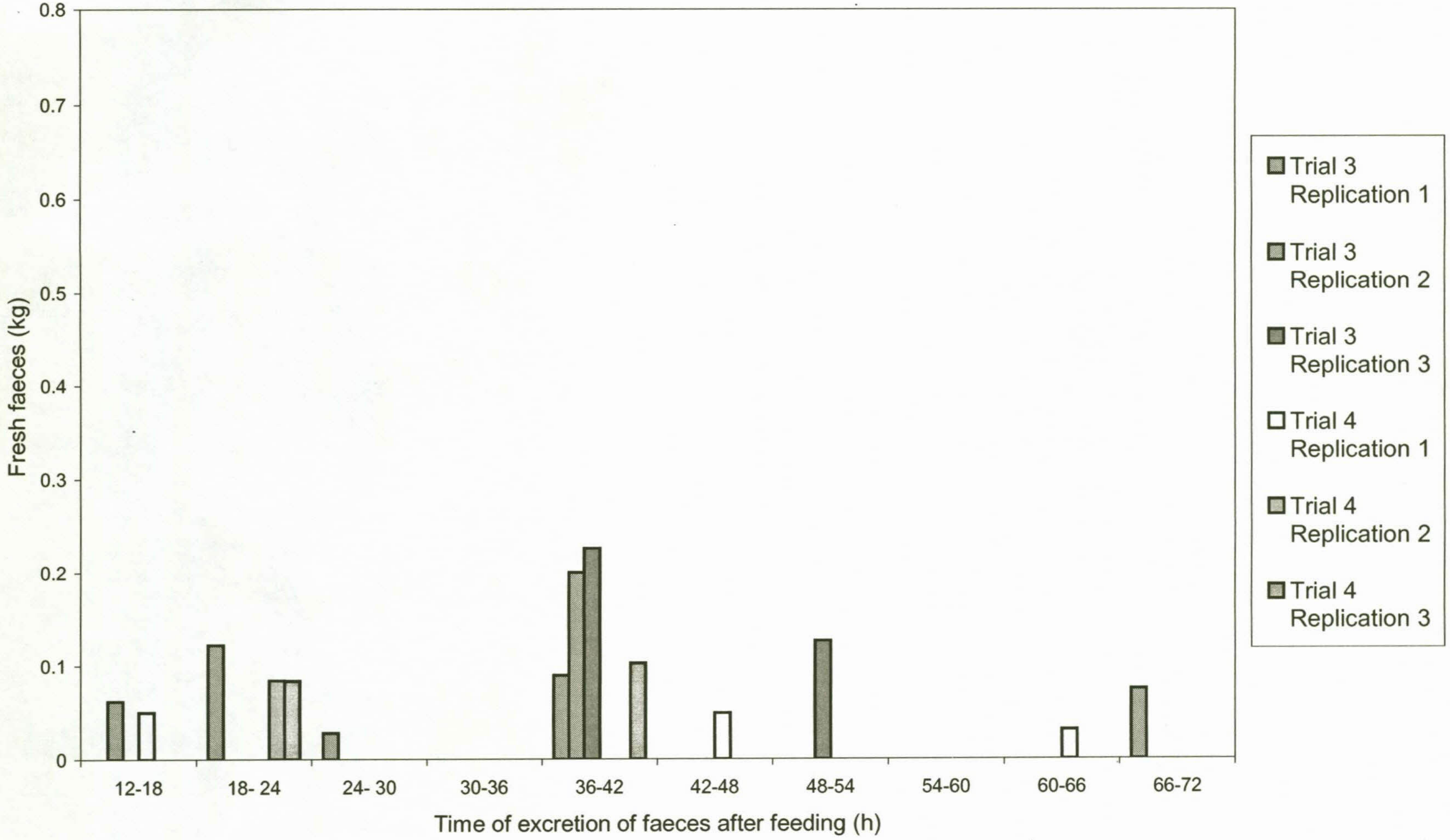

Figure 4.2.1 Fresh faeces (kg) excreted relative to feeding by a male (Trial 3) and female (Trial 4) leopard (*Panthera pardus*)

As was the case of the lions, the consistency and colour of the leopard scats changed throughout the collection period after feedings.

The regression lines of the mean increase in DM in later defecations are shown in Figure 4.2.2.

The increase in DM content of faeces is described by the following linear regression equations:

$y = 69.664X + 255.16$
$R^2 = 0.7463$ for the male leopard

and

$y = 92.068X + 168.97$
$R^2 = 0.9906$ for the female leopard.

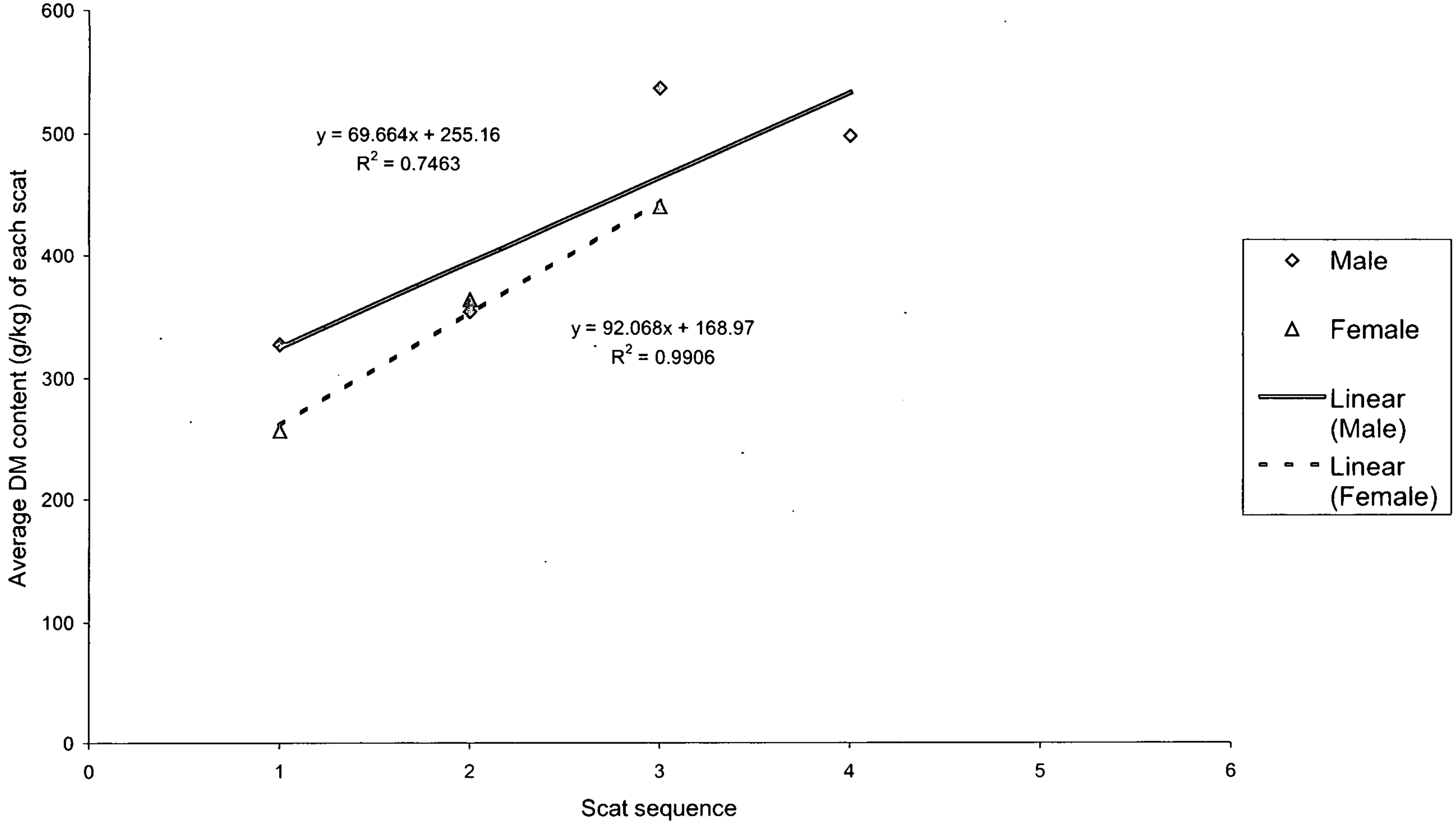

Figure 4.2.2 Regression line of faecal DM content (g/kg) for successive scats excreted by a male and female leopard (*Panthera pardus*) after feeding

The composition of the faeces excreted by the male and female leopard is shown in Table 4.2.8.

Table 4.2.8 Composition of faeces collected from a male and female leopard (*Panthera pardus*)

Trial	Predator	Replication	Dry matter (DM) (g/kg DM)	Crude protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (g/kg DM)	Gross Energy (GE) (MJ/kg DM)
3	Leopard male	1	375.843	542.900	34.939	281.214	23.330
		2	369.717	523.600	8.516	385.051	16.385
		3	514.077	672.900	9.164	324.101	16.244
4	Leopard female	1	353.101	541.900	11.235	291.047	18.764
		2	307.789	368.600	35.501	372.002	15.117
		3	273.827	347.300	32.342	279.272	19.241
	Mean		365.726	499.533	21.950	322.114	18.180
	SD		82.568	122.171	13.558	46.749	2.978
	CV		22.577	24.457	61.769	14.513	16.380

The mean faecal CP content of 499.533 g/kg shows the extent to which indigestible hair originating from the carcass portion passes through the digestive system. The low mean faecal lipid content of 21.950 g/kg shows the large extent to which lipids are digested and absorbed in the digestive tract. The faecal mineral content is largely due to the pieces of indigestible bone passing through the digestive tract. The mean faecal GE content of 18.180 MJ/kg shows the large extent to which GE is extracted from the diet.

4.3 Intake and digestibility studies with cheetah (*Acinonyx jubatus*)

Similar to the situation with lion and leopard, very little information is available on the quantitative nutrition, food intake and digestive capacity of the cheetah. In work done on essential fatty acid requirements of cheetahs, it was concluded that being obligate carnivores, cheetahs must eat sufficient amounts of animal lipid to maintain a healthy fatty acid balance (Davidson *et al.*, 1986).

4.3.1 Food intake and apparent digestibility

The larger bones and skin of prey is usually not eaten by cheetahs while feeding (Bothma & Walker, 1999). During the three trials done with the cheetah male, the skin was only once left uneaten. In two of the three trials the entire skin with hair was consumed. In the single trial done with the female cheetah the skin and hair was left uneaten. It was however noted on a separate occasion that the female did in fact consume the entire skin and hair of a meal. However, the large bones were left uneaten by both the male and female cheetahs.

The fresh food intake, faecal excretion and apparent digestibility of the trial diets for a male and female cheetah on a fresh (or as fed) basis are shown in Table 4.3.1.

Table 4.3.1 Fresh food intake, faecal excretion and the apparent digestibility of diets consisting of donkey or horse carcass portions (on a fresh, or as fed, basis) by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient	Replication	Fresh food intake (kg)	Fresh faeces excreted (kg)	Digestibility coefficient
1[*]	5.110	0.241	0.953	1[**]	5.621	0.309	0.957
2[*]	5.056	0.360	0.929			NA	
3[*]	6.184	0.327	0.947			NA	
Mean	5.450	0.309	0.943			NA	
SD	0.636	0.061	0.013			NA	
CV	11.674	19.805	1.326			NA	

[*] Horse carcass portion
[**] Donkey carcass portion
[NA] Not available due to zoo exchange program

The food intake, faecal excretion and apparent digestibilities of the trial diet on a dry matter (DM) basis by a male and female cheetah (*Acinonyx jubatus*) are shown in Table 4.3.2.

Table 4.3.2 Dry matter (DM) intake, faecal excretion and the apparent DM digestibility of diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient	Replication	Dry matter (DM) intake (kg)	Dry matter (DM) excreted (kg)	Digestibility coefficient
1*	1.333	0.090	0.933	1**	1.826	0.088	0.952
2*	1.368	0.118	0.914			NA	
3*	1.527	0.093	0.939			NA	
Mean	1.409	0.100	0.929			NA	
SD	0.103	0.015	0.013			NA	
CV	7.338	15.496	1.427			NA	

*Horse carcass portion
**Donkey carcass portion
NA Not available due to zoo exchange program

The low coefficients of variation found in these cases for the apparent digestibilities of fresh and DM in food (Tables 4.3.1 and 4.3.2) suggest that there was a high measure of repeatability in the techniques applied.

4.3.2 Nutrient intake and apparent digestibility

The composition of the food ingested by a male and female cheetah is shown in Table 4.3.3.

Table 4.3.3 Composition of the food intake from diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial	Predator	Replication	Dry matter (DM) (g/kg)	Crude protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (ash) (g/kg DM)	Gross energy (GE) (MJ/kg DM)
5	Male cheetah	13*	260.901	764.572	110.287	106.948	23.837
		14*	270.503	771.128	117.604	114.993	22.748
		15*	246.935	888.853	62.382	63.300	22.695
6	Female cheetah	16**	324.805	632.676	320.118	82.407	27.659
	Mean		275.786	764.307	152.598	91.912	24.235
	SD		34.082	104.698	114.334	23.578	2.343
	CV		12.358	13.698	74.925	25.653	9.667

*Horse carcass portion
**Donkey carcass potion

4.3.2.1 Crude protein (CP) intake and apparent digestibility

The CP intake, faecal excretion and apparent CP digestibility coefficients for a male and female cheetah are shown in Table 4.3.4.

As was the case with the lions and leopards, the high apparent digestibility of CP by cheetahs is reduced because of the large amount of hair excreted in the faeces. Hair, consisting of keratin, is largely indigestible and passes through the digestive tract of the predator unscathed by the hydrochloric acid secreted in the stomach and digestive enzymes of the carnivore digestive system. This has the implication that the hair protein does not contribute to the digestible protein fraction of the diet. Another factor contributing to the reduction of CP digestibility is the presence of metabolic faecal nitrogen originating from digestive enzymes, mucus and epithelial cells sloughed off the walls of the intestines by the passing digesta.

Some of the predator's own hair is also ingested through the act of grooming. This hair is also passed through the digestive system and ends up in the faeces making a further contribution to the undigested crude protein in the faecal material.

Table 4.3.4 Crude protein (CP) intake, faecal excretion and apparent CP digestibilities of diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	CP intake (kg)	CP excreted (kg)	Digestibility coefficient	Replication	CP intake (kg)	CP excreted (kg)	Digestibility coefficient
1*	1.019	0.047	0.954	1**	1.155	0.034	0.970
2*	1.055	0.075	0.929			NA	
3*	1.357	0.043	0.968			NA	
Mean	1.144	0.055	0.950			NA	
SD'	0.186	0.018	0.020			NA	
CV	16.243	32.308	2.130			NA	

* Horse carcass portion
** Donkey carcass portion
NA Not available due to zoo exchange program

On a number of occasions small amounts of undigested fresh blood originating from the predator was detected on the faeces. Sharp or coarse objects injuring the epithelial lining of the large intestine probably caused the bleeding. This phenomenon was observed in the lions, leopards, and cheetahs during this study. This will undoubtedly also contribute to some of the CP present in the faeces not originating from the ingested food and therefore reducing slightly the apparent CP digestibility coefficient.

4.3.2.2 Lipid intake and apparent digestibility

In a study done on essential fatty acid requirements of cheetah, it was concluded that being an obligate carnivore similar to the lion, leopard and domestic cat, cheetahs must eat sufficient amounts of animal lipid to maintain a healthy fatty acid balance (Davidson *et al.*, 1986). The lipid intake, faecal excretion and apparent lipid digestibility coefficients for a male and female cheetah are shown in Table 4.3.5.

Table 4.3.5 Lipid intake, faecal excretion and apparent lipid digestibility of diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient	Replication	Lipid intake (kg)	Lipid excreted (kg)	Digestibility coefficient
1*	0.147	0.002	0.983	1**	0.584	0.003	0.995
2*	0.161	0.002	0.989			NA	
3*	0.095	0.002	0.984			NA	
Mean	0.134	0.002	0.985			NA	
SD	0.035	0.000	0.003			NA	
CV	25.729	25.518	0.304			NA	

* Horse carcass portion
** Donkey carcass portion
NA Not available due to zoo exchange program

As was observed in the trials with male and female lions and leopards, the mean apparent lipid digestibility coefficients of the male and female cheetahs were also very high.

4.3.2.3 Intake and apparent digestibility of minerals (ash)

The mineral intake, faecal excretion and apparent mineral digestibility for a male and female cheetah are shown in Table 4.3.6.

The male cheetah was a sub-adult and still required relatively more minerals necessary for skeletal growth. The female was an adult and still has a fairly high mineral (ash) digestibility coefficient considering the fact that adult animals do not need a large amount of minerals for skeletal growth. Therefore, the conclusion could be made that cheetahs, being very fast animals, need more minerals such as calcium for muscle contraction and phosphorus for energy metabolism.

Table 4.3.6 Mineral intake, faecal excretion and apparent mineral digestibility of diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient	Replication	Mineral intake (kg)	Mineral excreted (kg)	Digestibility coefficient
1*	0.143	0.020	0.861	1**	0.150	0.029	0.808
2*	0.157	0.016	0.897	NA			
3*	0.097	0.019	0.802	NA			
Mean	0.132	0.018	0.853	NA			
SD	0.032	0.002	0.048	NA			
CV	23.922	10.315	5.623	NA			

* Horse carcass portion
** Donkey carcass portion
NA Not available due to zoo exchange program

The mean apparent mineral digestibility coefficients observed in the trials with the male (0.853) and female (0.808) cheetahs were relatively higher than the mean apparent mineral digestibility coefficients observed in the trials with male and female lions and leopards.

4.3.2.4 Gross energy (GE) intake and apparent digestibility

The GE intake, faecal excretion and apparent GE digestibility coefficients of diets by a male and female cheetah are shown in Table 4.3.7.

The mean GE intake was 32.516 MJ and 50.494 MJ for the male and female cheetah respectively. The mean GE excreted in the faeces was 2.182 MJ and 1.682 MJ for the male and female cheetah respectively. The mean apparent GE digestibility coefficients of diets by male and female cheetah were 0.932 and 0.967 respectively. The high apparent GE digestibility by cheetahs and also lions and leopards, is an indication of the high efficiency of energy utilisation from the carnivorous diet.

Table 4.3.7 Gross energy (GE) intake, faecal excretion and apparent GE digestibility of diets consisting of donkey or horse carcass portions by a male and female cheetah (*Acinonyx jubatus*)

Trial 5				Trial 6			
Male cheetah				Female cheetah			
Replication	Gross energy (GE) intake (MJ)	Gross energy (GE) excreted (MJ)	Digestibility coefficient	Replication	Gross energy (GE) intake (MJ)	Gross energy (GE) excreted (MJ)	Digestibility coefficient
1*	31.780	1.720	0.946	1**	50.494	1.682	0.967
2*	31.111	3.030	0.903	^{NA}			
3*	34.657	1.796	0.948	^{NA}			
Mean	32.516	2.182	0.932	^{NA}			
SD	1.884	0.735	0.026	^{NA}			
CV	5.794	33.677	2.752	^{NA}			

*Horse carcass portion
**Donkey carcass portion
^{NA}Not available due to zoo exchange program

The mean apparent GE digestibility coefficients observed for the male and female cheetahs were in line with those observed in the male and female lions and leopards in this study.

4.3.3 Excretion of faeces

The time intervals and faecal mass excreted by a male and female cheetah are shown in Figure 4.3.1.

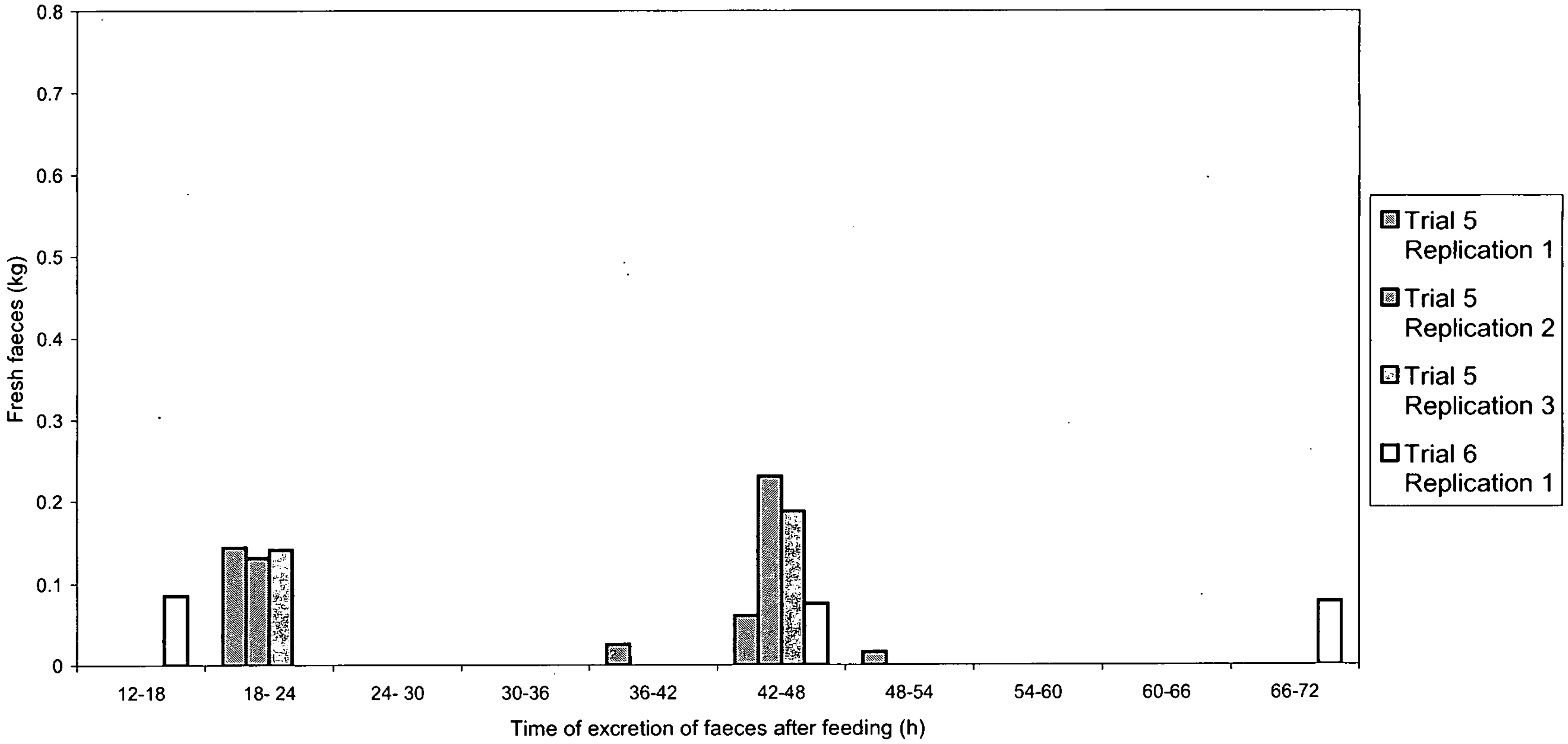

Figure 4.3.1 Fresh faeces (kg) excreted relative to feeding by a male (Trial 5) and female (Trial 6) (*Acinonyx jubatus*)

The regression lines for the DM content in the faeces with time in later defecations are shown in Figure 4.3.2.

As in the case of the lion and leopard, the consistency of the cheetah scat got changed from a soft almost fluid consistency to a harder, firm and "sausage-like" form. The colour changed throughout the collection period after feedings from a dark reddish brown to black to a dark brown to black colour.

The increase in DM content of faeces is described by the following linear regression equations:

$y = 45.239X + 236.74$
$R^2 = 0.7042$ for the male cheetah

and

$y = 76.113X + 213.87$
$R^2 = 0.9638$ for female cheetah.

The composition of the faeces excreted by the male and female cheetah is shown in Table 4.3.8.

Table 4.3.8 Composition of faeces collected from a male and female cheetah (*Acinonyx jubatus*)

Trial	Predator	Replication	Dry matter (DM) (g/kg)	Crude protein (CP) (g/kg DM)	Lipid (g/kg DM)	Minerals (g/kg DM)	Gross Energy (GE) (MJ/kg DM)
5	Male cheetah	1	371.970	522.800	27.833	221.323	19.191
		2	327.716	639.900	15.515	138.070	25.715
		3	282.998	462.100	16.456	207.221	19.413
6	Female cheetah	1	366.099	389.400	33.488	329.952	19.179
	Mean		337.196	503.550	23.323	224.141	20.875
	SD		41.118	106.003	8.790	79.369	3.229
	CV		12.194	21.051	37.688	35.410	15.468

The mean faecal CP content of 503.550 g/kg shows the extent to which indigestible hair originating from the carcass portion passes through the digestive system. The low mean faecal lipid content of 23.323 g/kg shows the large extent to which lipids are digested and absorbed in the digestive tract. The faecal mineral content is largely due to the pieces of indigestible bone passing through the digestive tract. The mean faecal GE content of 20.875 MJ/kg shows the extent to which GE is extracted from the diet. It can however be noted that the relatively higher GE content of the cheetah faeces is a result of the relatively lower apparent lipid digestibility by the cheetahs in this study allowing the passage of more lipids into the faeces resulting in a higher GE content.

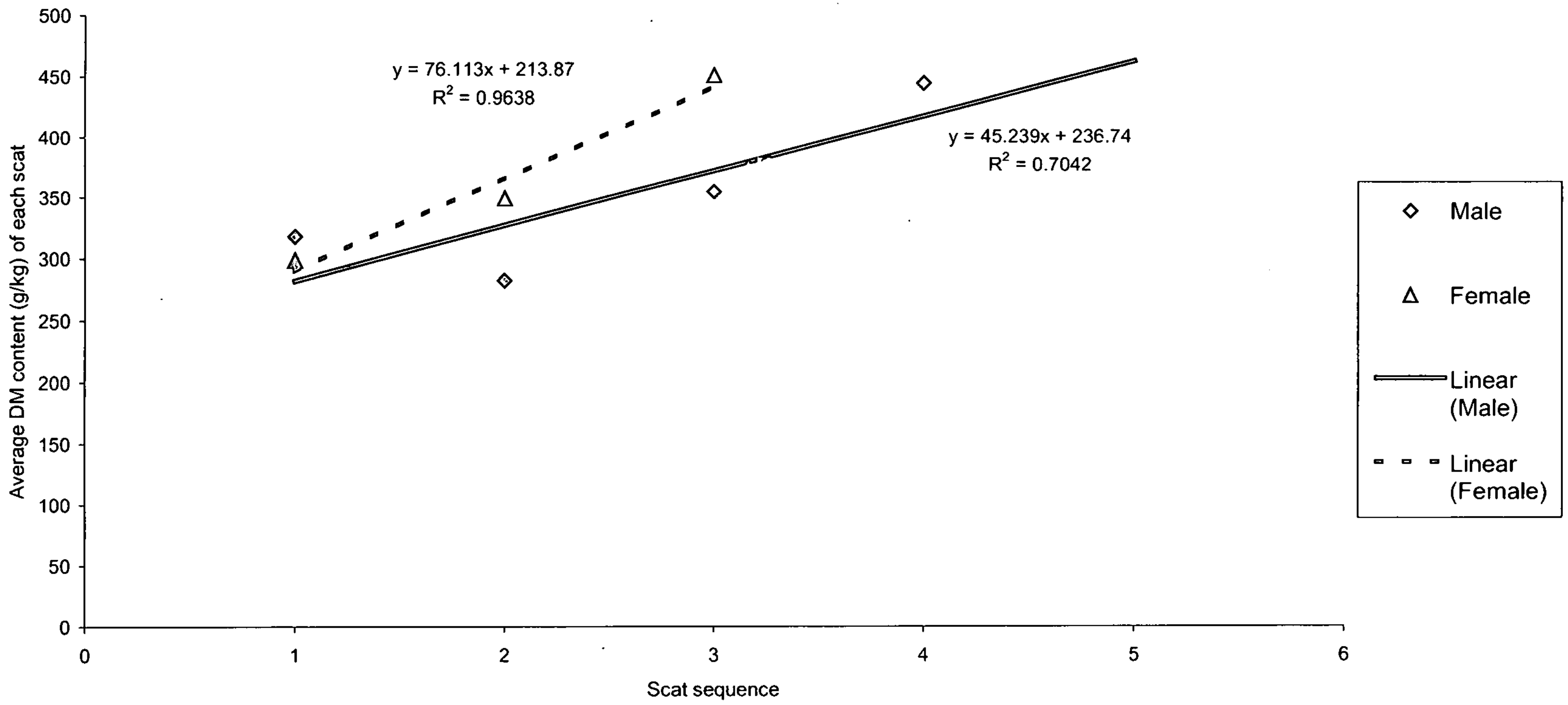

Figure 4.3.2 Regression line of faecal DM content (g/kg) for successive scats excreted by a male and female cheetah (*Acinonyx jubatus*) after feedings

4.4 Summary of comparative analyses on apparent digestibility coefficients of fresh food, dry matter (DM), lipid, minerals and gross energy (GE) of lions, leopards and cheetahs

A summary of the comparative analysis on the apparent digestibility coefficients of fresh food, DM, CP, lipid, minerals and GE of lions, leopards and cheetahs is shown in Table 4.4.

Table 4.4 Summary of comparative analyses on apparent digestibility coefficients of fresh food, dry matter (DM), crude protein (CP), lipid, mineral and gross energy (GE) of lions, leopards and cheetahs

	Predator species		
	Lion	Leopard	Cheetah
Variable		Mean ± SD	
Apparent digestibility of fresh food	0.909^{ns} ± 0.2080	0.954^{ns} ± 0.0114	0.950^{ns} ± 0.0102
Apparent DM digestibility	0.878^{ns} ± 0.0340	0.939^{ns} ±0.0263	0.940^{ns} ± 0.0165
Apparent CP digestibility	0.933^{ns} ± 0.0195	0.955^{ns} ± 0.0253	0.960^{ns} ± 0.0142
Apparent lipid digestibility	0.994^{ns} ± 0.0018	0.993^{ns} ± 0.0012	0.990^{ns} ± 0.0069
Apparent mineral digestibility	0.419^{ns} ± 0.1541	0.715^{ns} ± 0.1361	0.830^{ns} ± 0.0321
Apparent GE digestibility	0.935^{ns} ± 0.0073	0.952^{ns} ± 0.0189	0.949^{ns} ± 0.0244

^{ns} Means within rows do not differ significantly ($p>0.05$)
Data analysed by means of ANOVA (SAS, 1991)

From these results a conclusion could be made that there is no statistical difference ($p>0.05$) between the lions, leopards and cheetahs in this study in terms of the apparent digestibility of fresh food, dry matter, crude protein, lipid, mineral and gross energy. In general the digestibility coefficients are very high for all the nutrients considered in all three species. These results are in line with those of the literature on both domestic and wild cats.

4.5 Water intake derived from the trial diets by African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

The water content may account for 85% of the total mass of prey animal bodies (Green *et al.*, 1984). Predators may therefore obtain sufficient water from the blood and soft tissue of prey animals. Lions, leopards and cheetahs will, however, drink water regularly when it is available (Eloff, 1973; 1999; Green *et al.*, 1984; Bothma & Walker, 1999).

The estimated mean water intake derived from the trial diets by African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*) are shown in Table 4.5.

Table 4.5 Mean water intake derived from the trial diets by male and female African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

Predator	Mean water intake derived from the trial diets (kg)	Water intake as a percentage of body weight (%)	Water intake per metabolic size ($kg/kgW^{0.75}$)
Lion male	9.017	4.8	0.178
Lion female	8.488	6.6	0.222
Leopard male	4.077	7.7	0.208
Leopard female	2.527	7.2	0.177
Cheetah male	4.041	10.0	0.252
Cheetah female	3.795	NA	NA

NA Not available

This information confirms that large African predators obtain a considerable amount of water from their diets. If the results are expressed as a percentage of body mass it appears as if the water intake from the diets increases with smaller body mass. However, no trend is visible when the water intake from the diet is expressed per metabolic size.

4.6 Practical implications

4.6.1 Mineral and vitamin supplementation

Meat is a good source of minerals, especially iron, phosphorus, copper and manganese. Muscle is generally low in calcium, but blood plasma and especially bone have high calcium contents (McDonald *et al.*, 1995).

It is common practice at some institutions such as zoos and game farms where carnivores are kept in captivity to supplement the mineral intake of carnivores with bone meal or commercial mineral supplementations. In the case of lions it would seem that the fairly low digestibility of minerals (ash) is reason to believe that the supplementation of especially adult animals is not necessary. Leopards and cheetahs however have higher apparent digestibilities of minerals (ash). It may therefore be concluded, especially in the case of captive cheetahs, that mineral supplementation may by worthwhile to prevent mineral deficiencies. These animals cannot crush large bones offered to them.

Meat is a fair to good source of the vitamin B complex and a fair to good source of all the fat-soluble vitamins (McDonald *et al.*, 1995). Raw animal liver and oils from livers of certain fish, especially cod and halibut are good sources of vitamin A and E (McDonald *et al.*, 1995). The supplementation of the diet of young, sick or stressed animals (due to transport, new environment etc.) with raw liver is recommended as a cheap and effective means of providing the necessary minerals and vitamins.

4.6.2 Determination of food intake of free-ranging predators

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 faecal excretion of a large predator, the intake of the animal can be estimated by using the following equation:

$$FFI = (TFC)/(1-ADC)$$

FFI= Fresh food intake (kg)

TFC= Total fresh faeces excreted (and collected) (kg)

ADC= Apparent digestibility coefficient

Similarly, if the DM digestibility coefficient is known, the DM intake (DMI) can be estimated with the following equation:

$$\mathrm{DMI} = (\mathrm{TFC})/(1-\mathrm{ADC})$$

Where DMI= Dry matter intake (kg)

$\mathrm{TFC}_{\mathrm{DM}}$= Total dry faecal collection (kg DM)

$\mathrm{ADC}_{\mathrm{DM}}$= Apparent DM digestibility coefficient

If for example, the mean apparent digestibility coefficient (ADC) of food (in this case donkey or horse carcass portions) on an as fed or fresh basis is known to be 0.889 and the total faecal collection (TFC) of that particular meal yielded 1.499 kg of fresh faeces, the fresh food intake (DMI) of that particular predator could be estimated as 13.51 kg.

Due to the varying time it may take to safely collect fresh faeces and the varying rate of evaporation of water from the faeces during the time of deposition and collection it should be noted that the equation for DM values should be given preference in estimating intake.

This is a much more accurate way of determining food intake than simply estimating the intake of predators. The disadvantage of using this suggested procedure is that a particular predator must be observed and tracked to be able to keep note of feedings and subsequent dropping of faeces. All the faeces of a particular animal must be collected in order to make an accurate intake calculation. Recent studies on techniques for the collection of lion scat show that it is possible to collect the total scat excretion of predators outside a zoo environment (Yanna Smith & H.O. de Waal, 2002, personal communication). This method will be useful in the estimation of DM intake of free-ranging large African predators. Work is currently in progress to do further refinement of various techniques in this regard.

5 Conclusions and recommendations

5.1 Conclusions

The non-invasive techniques developed and applied for determining food intake and apparent digestibility for large African predators in captivity in this study are feasible and accurate. These techniques have great potential to be used also in the wild with free roaming predators provided that the faecal samples of individual animals can be marked for identification and all the scat are collected.

The results of the intake and digestibility trials with the African lion, the leopard and the cheetah have shown that these obligate carnivores are well adapted to ingest and digest meat - their typical carnivorous diets. Although the large wild cats in general and the lions in particular are adapted to a feast and famine lifestyle, these animals utilise their food and, therefore, its nutrient content efficiently.

The diet of carnivores is relatively high and constant with respect to its water content, which may account for up to 85% of the bodies of prey animals. The results of this study have also shown that these large carnivores obtain large quantities of water from their diet. This supports other field studies that reported that roaming lions could survive for long periods of time without drinking water. Predators therefore obtain considerable amounts of water from the blood and soft tissue of prey animals. The high water extraction and retention by carnivores relative to their metabolic weight strengthens the theory that even though predators living in arid areas can only drink water when it is available, they can survive long periods of water shortages by utilising the water from the carcasses of prey animals.

The high apparent digestibility of CP is of great importance in the nutrition of carnivores. Protein comprises the main component of meat and is the most important nutrient of carnivores. In the liver, some of the nitrogen containing amino acids is catabolised to ammonia and keto-acids. The ammonia is converted to urea in the liver and excreted via the kidneys while the keto-acids are converted into glucose and utilised as a major source of energy (McDonald *et al.,* 1995). Protein thus provides the amino acid requirements of the large cats and also serves as an energy source. Although lipids contain 2.25 times the energy content of carbohydrates and animal fat contains 1.67 times the energy content of muscle. Fat is consumed in smaller quantities than muscle and is therefore the second most important energy source of carnivores.

In this study it was observed that the lions, leopards and cheetahs ingested a small amount of green grass. Eating small amounts of green grass is common amongst carnivores. Lions are also known to ingest grass from time to time. The amount of grass ingested by lions may be at times substantial. Smuts (1978) reported that a particular female ingested 200 g of green grass. This occurred when little or no hair originating from the skin of the carcass portion was ingested or available to ingest. The hair and grass are indigestible and therefore have no nutritional importance to predators such as cats, but presumably act as natural laxatives to purge the digestive track of old and dead epithelial cells. The CP content of the faeces was elevated by the large quantities of indigestible hair contained in the diet.

The very high apparent digestibility of lipids is an indication that lions, leopards, cheetahs and other members of the cat family are very well adapted to digest and absorb almost all of the fat ingested from the diet to provide energy as well as the essential fatty acid requirements. A further positive implication of the very high apparent digestibility of lipid is the effective absorption of the fat-soluble vitamins A, D, E and K.

Throughout the study it was found that the lions have a lower apparent digestibility of the dietary mineral component (ash) than the leopards and cheetahs. This may be due to the fact that lions eat more bone than leopards and cheetahs, which leads to more indigestible bone fragments ending up in the faeces, effectively lowering the apparent mineral digestibility. The mineral content of the diet is inversely related to the total energy content of the diet, which entails that when a predator ingests a larger proportion of bone relative to muscle and fat, the intake of energy is reduced. However, when a large quantity of fatty bone marrow is ingested with the bone mineral matter, the dilution effect of the high mineral content of the bone is counteracted; provided a predator does not selectively feed on prey in poor condition due to age, starvation or disease.

The apparent digestibility of energy by all three species was very high. This implies that although none of these predators are very successful hunters and spend great amounts of energy during the hunting activity to catch prey, the energy derived from the diet is absorbed to a great extent to compensate the energy invested for hunting.

The energy intake by carnivores varies considerably according to the composition of the diet and body condition of their prey. Therefore the body condition of the prey animals consumed plays an important role in the nutritional and energy status of the predators.

The use of apparent digestibility coefficients for fresh food and DM can be very useful as a method to determine the actual fresh food and DM intake of predators. This entails that when the preferred prey species of a particular predator is known, the apparent DM digestibility coefficient obtained by a particular predator species for the prey species can be used to estimate the DM intake of the predator from the total dry faecal mass originating from a specific feeding. This is a more accurate way of determining DM intake than previous estimations.

When the actual DM intake of a particular predator population in a certain area is known the management in terms of size of prey population necessary to sustain the predator population can be accurately estimated. This information will be particularly useful in areas where predator-prey ratios are controllable, as is the case on game farms and nature reserves. The methods developed and used in this study were developed with the specific goal to be later used in all areas where predators are ranging freely.

5.2 Recommendations

Future challenges in the development of non-invasive techniques to conduct nutritional studies on large carnivores are to:

- determine the exact food and nutrient requirements for large African carnivores.
- develop more reliable ways of external marking of carnivore diets to ensure better identification of faeces.
- develop reliable methods of collecting fresh faecal matter from free-ranging predators.
- improve the methods of carcass processing in preparation for laboratory analysis to minimize water loss due to grinding friction.
- determine possible effects of intake on digestibility.

If the information is available and the techniques described above are applied judiciously, it might be possible to determine the food and nutrient intake of large African predators. This will enable us to determine in a non-invasive manner the nutritional status of large African predators in the different physiological stages of their lives.

Abstract

Intake and digestibility studies with captive African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

By

Dirk Gerber Borstlap

Supervisor: Prof. H.O. de Waal (University of the Free State)
Co-supervisor: Dr L.M.L. Schwalbach (University of the Free State)

Degree: MSc Agric

The long-term goal of this study of the quantitative nutrition of large African predators was to develop non-invasive techniques for the accurate determination of food intake and apparent nutrient digestibility by free-ranging predators.

The specific objectives of this study were to:

- develop non-invasive techniques to determine the apparent digestibility of fresh, non-processed food by three species of large African predators.
- determine the apparent dry matter (DM) digestibility of typical carnivorous diets in terms of DM, crude protein (CP), minerals, fat and gross energy (GE).
- obtain information on the digestive capabilities and the water retention in three species of large African predators.
- lay the basis for developing a technique to determine the food intake on a nutrient basis by free-ranging large African predators.

This study was conducted in the Bloemfontein Zoological Gardens (Bloemfontein Zoo) with paired captive male and female African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*). Although the study was done with captive animals the techniques were developed in such a manner that its principles would be applicable in the uncontrolled environment of free-ranging predators. The study consisted complete intake and

digestibility trials conducted and repeated three times respectively on a male and a female of each of the three predator species.

The trial diets consisted of portions of the limbs from either adult donkeys (*Equus asinus*) or a horse (*Equus caballus*). The trial carcass portions used consisted of two symmetrical and identical portions or cuts that were divided in different sections, *e.g.* the two front limbs or the two hind limbs originating from the same carcass. One carcass portion was fed to a specific predator as the trial diet and the mirror image carcass portion was retained for nutrient analysis in the laboratory. The trail diets were marked using maize seeds (*Zea mays*) as external marker to assist in the faecal identification and facilitate collection. After feeding a ration, total faecal and food refusal collections were made.

The intake and apparent digestibility of the fresh food, DM and nutrients were determined using standard laboratory techniques. The results of the intake and digestibility trials with the African lion, the leopard and the cheetah have shown that these carnivores are well adapted for the ingestion and digestion of meat.

Mean DM intakes ranged from 0.970 kg for a female leopard to 4.493 kg for a male lion. The mean apparent DM digestibility ranged from 0.854 to 0.957. Nutrients such as CP, lipid and GE had very high apparent digestibility coefficients by the predators ranging from 0.919 to 0.977 for CP, 0.983 to 0.995 for lipid and 0.918 to 0.967 for GE respectively. The apparent digestibility of minerals (ash) was lower ranging from 0.310 to 0.853.

From this analysis the conclusion could be made that there is no statistical difference between the lions, leopards and cheetahs in this study in terms of the apparent digestibility of fresh food, dry matter (DM), crude protein (CP), lipids, minerals and gross energy (GE). This study also confirmed that large African predators obtain a considerable amount of water from their diets.

The use of apparent digestibility coefficients for fresh food and DM can be a very useful method to estimate the actual food intake (on a fresh or DM basis) of carnivores. If the information is available and the techniques described are applied judiciously, it might be possible to estimate the food and nutrient intake of large African predators. Evaluation of the nutritional status of large African predators during the different physiological stages of their lives in a non-invasive manner will thus be possible. It will also provide scientific support to devise adequate, sustainable and holistic management practices to preserve both the large African carnivores and the environment that supports their existence.

Samevatting

Intake and digestibility studies with captive African lions (*Panthera leo*), leopards (*Panthera pardus*) and cheetahs (*Acinonyx jubatus*)

deur

Dirk Gerber Borstlap

Studieleier:	Prof. H.O. de Waal (Universiteit van die Vrystaat)
Mede-studieleier:	Dr L.M.L. Schwalbach (Universiteit van die Vrystaat)

Graad: MSc Agric

Die langtermyn doel van hierdie studie van die kwantitatiewe voeding van groot Afrika roofdiere was die ontwikkeling van nie-indringende tegnieke vir die akkurate bepaling van die voedselinname en skynbare voedingstof verteerbaarheid deur vrylewende roofdiere.

Die spesifieke doelstellings van hierdie studie was die:

- ontwikkeling van nie-indringende tegnieke vir die bepaling van die skynbare verteerbaarheid van vars, ongeprosesseerde voedsel deur drie groot Afrika roofdierspesies.
- bepaling van die skynbare droëmateriaal (DM) verteerbaarheid van tipiese karnivoordiëte in terme van DM, ruproteïen (RP), minerale, lipiede en bruto-energie (BE).
- insameling van inligting rondom die verteringsvermoë en die water retensie in hierdie drie spesies groot Afrika roofdiere.
- skep van 'n basis vir die ontwikkeling van 'n tegniek vir die bepaling van die voedselinname op 'n voedingstofvlak deur vrylewende groot Afrika roofdiere.

Hierdie studie is in die Bloemfontein Dieretuin op pare manlike- en vroulike Afrika roofdiere in gevangenskap uitgevoer naamlik; Afrika leeus (*Panthera leo*), luiperds (*Panthera pardus*) en jagluiperds (*Acinonyx jubatus*). Alhoewel die studie op roofdiere in gevangenskap gedoen is, is die tegnieke op so 'n wyse ontwikkel dat die beginsels toepaslik sal wees in die

onbeheerbare omgewing van vrylewende roofdiere. Die studie, bestaande uit 16 volledige inname- en verteringstudies is met 'n manlike- en vroulike dier van elk van die drie roofdierspesies uitgevoer en is drie keer herhaal.

Die toetsdiëte het uit gedeeltes van die ledemate van volwasse donkies (*Equus asinus*) of 'n perd (*Equus caballus*) bestaan. Die toetskarkasporsies het uit twee simmetriese en identiese gedeeltes of snitte wat in verskillende gedeeltes opgedeel is bestaan, bv. die twee voorbene of agterbene afkomstig van dieselfde karkas. Een karkasporsie is aan 'n spesifieke roofdier gevoer as toetsdieet en die spieëlbeeldkarkasporsie is bewaar vir voedingstofanalise in die laboratorium. Die toetsdiëte is met mieliepitte (*Zea mays*) as eksterne merker gemerk om die misidentifikasie en -kolleksies te vergemaklik. Totale miskolleksies sowel as kolleksies van die voerreste is na 'n voeding gemaak.

Die inname en skynbare verteerbaarheid van die vars voedsel, DM en voedingstowwe is bepaal met behulp van standaard laboratorium tegnieke. Die resultate van die inname en verteringstudies met die Afrika leeus, luiperds en jagluiperds het aangetoon dat hierdie karnivore goed aangepas is tot die inname en vertering vleis.

Gemiddelde DM innames het gestrek van 0.970 kg vir die luiperdwyfie tot 4.493 kg vir die leeumannetjie. Die gemiddelde skynbare DM verteerbaarheid het van 0.854 tot 0.957 gestrek. Baie hoë skynbare verteerbaarheidskoëffisiënte vir voedingstowwe soos RP, lipiede en BE is deur die roofdiere behaal en het gestrek vanaf 0.919 tot 0.977 vir RP, 0.983 tot 0.995 vir lipiede en 0.918 tot 0.967 vir BE respektiewelik. Die skynbare verteerbaarheid van minerale (as) was laer en het gestrek vanaf 0.310 tot 0.853.

Vanaf die data analise kon die gevolgtrekking gemaak word dat daar geen statistiese verskille tussen die drie roofdier spesies in terme van skynbare verteerbaarhede van vars voedsel, droëmateriaal (DM), ruproteïen (RP), lipiede, minerale en bruto-energie (GE) was nie. Hierdie studie bevestig ook dat groot Afrika -roofdiere 'n aansienlike hoeveelheid water vanaf hulle dieet verkry.

Die gebruik van skynbare verteerbaarheidskoëffisiënte vir vars voedsel en DM kan baie nuttig wees as 'n metode vir die beraming van voedselinname (i.t.v. vars of 'n DM-basid). Indien die inligting beskikbaar is en die tegnieke soos beskryf verstandig gebruik word, mag dit moontlik wees om die voedsel- en DM-inname sowel as die voedingstofinname van groot Afrika roofdiere te beraam. Dit sal ons in staat stel om op 'n nie-indringende wyse die voedingsstatus van groot Afrika-roofdiere in 'n verskeie fisiologiese stadia te evalueer en om wetenskaplike ondersteuning te verskaf vir die afleiding van geskikte, holistiese en volhoubare bestuurspraktyke om sodoende beide die groot Afrika roofdiere en die omgewing wat hulle bestaan onderhou te bewaar.

List of key words

Intake and digestibility studies
Apparent digestibility
Food intake
Water intake
Captive large predators
African lion (*Panthera leo*)
Leopard (*Panthera pardus*)
Cheetah (*Acinonyx jubatus*)
Carcass composition
Nutrient content
Faecal excretion

References

AOAC, 2000. *In:* Horwitz, W. (ed.) *Official Methods of Analysis of AOAC International.* Volume 1. 17th Edition. AOAC International ®.

Barbiers, R.B., Vosburgh, L.M., Ku, P.K. & Ullrey, D.E., 1982. Digestive efficiencies and maintenance energy requirements of captive wild Felidae: cougar (*Felis concolor*); leopard (*Panthera pardus*); lion (*Panthera leo*); and tiger (*Panthera tigris*). *Journal of Zoo Animal Medicine* 13, 32-37.

Bertram, B.R., 1975. The social system of lions. *Scientific American* 232, 54-65.

Bothma, J. du P., 1997. Larger carnivores on game ranches. *In: Proceedings of a Symposium on Lions and Leopards as Game Animals*. 24 & 25 October 1997. Ed. J. van Heerden. Onderstepoort, Republic of South Africa. pp 58-81.

Bothma, J. du P. & Le Riche, E.A.N., 1989. Evidence of a flexible hunting technique in Kalahari leopards. *South African Journal of Wildlife Research* 19(2), 57-60.

Bothma, J. du P. & Le Riche, E.A.N., 1994. Scat analysis and aspects of defecation in northern Cape leopards. *South African Journal of Wildlife Research* 24(1&2), 21-25.

Bothma, J. du P. & Walker, C., 1999. *Larger Carnivores of the African Savannas*, J.L. van Schaik Publishers, Pretoria.

Caro, T.M., 1982. A record of cheetah scavenging in the Serengeti. *African Journal of Ecology* 20, 213-214.

Clark, C.W., 1987. The lazy adaptable lions: a Markovian model of group foraging. *Animal Behaviour* 35, 361-368.

Davidson, B.C., Cantrill, R.C. & Varaday, D., 1986. The reversal of essential fatty acid deficiency symptoms in cheetah. *South African Journal of Zoology* 21, 161-164.

Eaton, R.I., 1974. *The cheetah; the biology, ecology, and behaviour of an endangered species*, Van Nostrand Reinhold Company, New York.

Eloff, F.C., 1973. Lion predation in the Kalahari Gemsbok Park. *Journal of the South African Wildlife Management* 3(2), 59-63.

Eloff, F.C., 1973. Water use by the Kalahari lion *Panthera leo vernayi*. *Kudu* 16, 149-54.

Eloff, F.C., 1977. Seven days with a lion family. *Custos* 6(4), 6-7,17,32.

Eloff, F.C., 1980. Cub mortality in the Kalahari lion (*Panthera leo vernayi*) (Roberts 1948) *Kudu* 3,163-170.

Eloff, F.C., 1999. Jagters van die duine. Die storie van die Kalaharileeu [*Hunters of the dunes. The story of the Kalahari lion.]* J.L. Van Schaik, Hatfield, Pretoria.

Godber, J.S., 1994. Nutritional value of muscle foods. In: Muscle Foods. Ed. Kinsman, D.M., Cotulla, A.W., Breidenstein, B.C. Chapman & Hall, New York. London.

Green, B., Anderson, J. & Whateley, T., 1984. Water and sodium turnover and estimated food consumption in free-living lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*). *Journal of Mammalogy* 65(4), 593-599.

Kendall, P.T., Holme, D.W. & Smith, P.M., 1982. Comparative evaluation of net digestive and absorptive efficiency in dogs and cats fed a variety of contrasting diet types. *The journal of small animal practice* 23, 577-587.

Kruuk, H. & Turner, M., 1967. Comparative notes on the predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* 31(1), 1-27.

Leco, 2001. FP-528 Protein/Nitrogen Determinator. *FP-528 Instruction Manual*, Version 1.2. Leco ® Corporation.

Marker, L., Kraus, D., Barnett, D. & Hurlbut, S., 1996. *Cheetah survival on Namibian Farmlands.* Second Edition, Cheetah Conservation Fund (CCF).

McBride, C.J., 1982. Age and size categories of lion prey in Chobe National Park, Botswana. *Botswana Notes and Records* 16, 139-143.

McDonald, P., Edwards, R.A., Greenhalgh, J.F.D. & Morgan, C.A., 1995. *Animal Nutrition.* Fifth Edition, Longman Singapore Publishers (Pty) Ltd., Singapore.

Mills, M.G.L., 1984. Prey selection and feeding habits of the large carnivores in the southern Kalahari. *Koedoe (Supplement)* 27, 281-294.

Mills, M.G.L., 1996. Methodological advances in capture, census, and food-habits studies of large African carnivores. *In:* Gittleman, J.L. (ed.). *Carnivore behavior, ecology and evolution.* Vol. 2. Cornell University Press, Ithaca, New York. pp 223-242.

Mills, M.G.L. & Biggs, H.C., 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. *Symposium of the Zoological Society of London* 65, 253-268.

Morris, J.G., Fujimoto, J. & Berry, S.C., 1974. The Comparative digestibility of a zoo diet fed to 13 species of felid and a badger. *International Zoo Yearbook.* pp 169-171.

Packer, C., Scheel, D. & Pusey, A.E., 1990. Why lions form groups: food is not enough. *The American Naturalist* 136(1), 1-19.

Pienaar, U. de V., 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12, 108-176.

Powers, J.G., Mautz, W.W. & Perkins, P.J., 1989. Nutrient and energy assimilation of prey by bobcats. *Journal of Wildlife Management* 53(4), 1004-1008.

SAS Institute Inc., 1991. SAS/STAT® Software: Usage and reference, Version 6.04. Cary, NC: SAS Institute Inc., 1991.

Schaller, G.B., 1969. Life with the king of the beasts. *National Geographic Magazine* 135(4), 494-519.

Schaller, G.B., 1972. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago

Schaller, G.B., 1972a. Predators of the Serengeti: Part 1; The Social Carnivore. *Natural History* 81(2), 38-49.

Schaller, G.B., 1972b. Predators of the Serengeti: Part 2; Are you running with me, hominid? *Natural History* 83(2), 61-69.

Schaller, G.B., 1972c. The endless race of life: Part 3. *Natural History* 81(4), 38-42.

Scot, P.P., 1998. The special features of nutrition of cats, with observations on wild felidae nutrition in the London Zoo. *Symposium of the Zoological Society of London* 21, 21-36.

Skinner, J.D. & Smithers, R.H.N., 1990. *The Mammals of the Southern African Subregion*, University of Pretoria, Pretoria.

Smuts, G.L., 1979. Diet of lions and spotted hyaenas assessed from stomach contents. *South African Journal of Wildlife Research* 9, 19-25.

Smuts, G.L., Robertson, G.A.& Whyte, I.J., 1980. Comparative growth of wild male and female lions (*Panthera leo*). *Journal of Zoology, London* 190, 365-373.

Stander, P.E., 1992. Foraging dynamics of lions in a semi-arid environment. *Canadian Journal of Zoology* 70, 8-21.

Stander, P.E., 1997. The ecology of lions and conflict with people in North-Eastern Namibia. *Proceedings of a Symposium on Lions and Leopards as Game Ranch animals*. Ed. Van Heerden, J, Wildlife Group of the South African Veterinary Association, Onderstepoort, Pretoria. pp 10-17.

Van Orsdol, K.G., 1982. Ranges and food habits of lions in Rwenzori National Park, Uganda. *Symposium of the Zoological Society of London* 49, 325-340.

Van Valkenburgh, B., 1989. Carnivore dental adaptations and diet: A study of trophic diversity within guilds. In: Carnivore behaviour, ecology and evolution. Ed. Gittleman, J.L., Cornell University Press, New York.

Viljoen, P.C., 1993. The effects of changes in prey availability on lion predation in a large natural ecosystem in northern Botswana. *Symposium of the Zoological Society of London* 65,193-213.

Appendix

Protocol to conduct digestibility trials with captive large African predators

This protocol was used to conduct the intake and digestibility studies in the Bloemfontein Zoological gardens. This protocol is a step-by-step guide to conduct similar studies on large predators in captivity. In these trials it is endeavoured that the feeding routine of the predators will not be interrupted or upset. This means that the current feeding routine will be followed to avoid upsetting the feeding routine of the predators.

1.1 Preparation of the trial diets (carcass portions)

List of equipment:

Donkey/horse carcass or other "prey species"
Commercial meat saw
Freezer
Large butcher's knife
Laboratory scale (4 decimal)
Large butcher's scale
Maize and/or lentil seeds
Large plastic bags

Step 1/1.1: Separate the hind limbs from the eviscerated carcass by cutting between the last lumbar and first sacral vertebrae before the pelvis.

Step 2/1.1: Separate the two hind limbs (hindquarters) by using a commercial meat saw to cut through the length of the sacral vertebrae. This will yield two mirror images of a hindquarter each. The lower part of the hind leg was removed by cutting through the joint just below the tibia.

Another method to separate the hind limbs from the carcass is to simply cut through the joint between the femur and the pelvic bone.

The fore limbs are removed by cutting alongside the ribcage to separate the two mirror image fore limbs from the carcass.

The lower part of the front leg is removed by using a commercial meat saw to cut just below the ulna.

One of the hindquarters/mirror image fore limbs (trial diet) will be fed to the predator and the other (mirror image carcass portion) will be retained in the laboratory for analysis (**See 1.4**).

Step 3/1.1: Weigh each trial diet accurately to determine the weight of the trial diet as fed. The weight of the trial diet must be similar to the weight usually consumed by the predator.
Step 4/1.1: Place the mirror image carcass portion into a large plastic bag and mark for easy identification. Freeze and store the whole mirror image carcass portion at –10°C.

The trial diet to be fed to the "tester" predators must now be marked with external markers using maize and/or lentil seeds.

Step 5/1.1: Weigh and record the mass (**A**) of ten seeds. By using a sharp knife to punch holes into the meat of the trial diet to insert the maize/lentil seeds into the soft tissue of the prepared hindquarter. This procedure will only apply when more than one predator is present in the enclosure. The "filler" predator will be fed chicken tripe, whole chicken or a skinned ribcage.

The above-mentioned procedure will be performed while the carcass is still fresh to avoid the water drainage caused when frozen meat is thawed.
If more than one predator is used as "tester" predators, two similar hindquarters will be prepared in the same manner as previously described. A different marker will be used for each of the two "tester" predators.

1.2 Feeding the prepared hindquarter to the "tester" predator

List of equipment:
Scale to weigh predators
Prepared trial diets (**see 1.1**)
Laboratory scale to weigh food refusals (1 decimal)
Plastic bags that can seal and permanent water resistant marker
Freezer

Day 1

Step1/1.2: Before any feeding commences, the night chambers and leisure yards must be cleaned of all faeces and leftover food of previous feedings.

Step 2/1.2: Weigh the predators and record the body mass.

Step 3/1.2: Lure the predators into their separate overnight cages and close the steel grate doors.

Step 4/1.2: Place the "filler" predator's food in the leisure yard and let the "filler" predator out.

Step 5/1.2: The prepared trial diet (**see 1.1**) will now be fed to the "tester" predator.

Step 6/1.2: Record the time when the feeding is started.

1.2.1. Care must be taken to ensure that no exchange of food occurs between the predators where more than one is present in a specific facility.

Step 6/1.2: Leave the food with the predators overnight.

Day 2

Step 7.12: Lure the "tester" and "filler" predators into separate chambers, close the grate doors and clear the leisure yard of all faeces and food refusals of the "filler" animal.

Step 7/1.2: Let the predators out of the overnight cages and close the steel grate doors.

Step 8/1.2: Remove and weigh the food refusals of the "tester" predator.

Step 9/1.2: Place food refusals of the different predators in well-marked plastic bags, and seal.

Step 10/1.2: Freeze and store the food refusals at – 10°C.

Day 1-2.

Step 11/1.2: Without disturbing the predators observe the predators to record the time of the production of the first faeces (this will be called the minimum retention time) until the last faeces is produced.

Step 12/1.2: Lure the predators into the overnight cages and close the steel grate doors.

Step 13/1.2: Remove all the faeces of the "tester" predators and put in separate sealable bags.

Step 14/1.2: Weigh and record total faeces produced for each of the predators separately (**A**).

1.2.3 The type of external marker present (e.g. maize seeds) will be used to identify the faeces of each predator.

1.2.4 An attempt must be made to collect the faeces as fresh as possible to minimize moisture loss.

Step 15/1.2: Collect and weigh the seeds (maize or lentil seeds) from the faeces (B).

Step 16/1.2: Determine the total corrected faeces mass (C) as follows:

$$\mathbf{C = A\text{-}B}$$

Step 17/1.2: Place each the faeces of each predator in separate well-marked plastic bags and freeze at –10°C.

1.3 Preparation of collected faeces for chemical analysis (see step 13/1.2.)

List of equipment:

Stainless steel pans

Laboratory scale to weigh samples (2 decimals).

Desiccators

Forced air drying oven

Grinder with 0.75 mm sieves to grind samples (Dietz Motoren KG, 1.1 KW, 2840 min)

Step 1/1.3: Tare the scale and weigh the stainless steel pans and record the mass (**A**).

Step 2/1.3: Place the faeces on the pan. Record the mass (**B**).

Step 3/1.3: Place in forced air drying oven at 100°C overnight.

Step 4/1.3: After drying, place the pan and faeces in desiccator until cool and weigh (**C**).

Step 5/1.3: Determine DM content (g/kg) of each sample as well as the mean DM content.

$$\text{DM (g/kg)} = (C - A) / (B\text{-}A)*1000$$

Step 6/1.3: Determine the mean DM content for the faeces.

Step 7.1.3: Grind the dried faeces through a 0.75 mm sieve, mix thoroughly, take a representative sample and place in a 250 ml bottle with a screw on lid.

1.4 Preparation of the mirror image carcass portion and food refusals for chemical analysis

List of equipment:

Commercial meat saw

Wolf carcass grinder

Scraper

Laboratory scale (2 decimals)

Grinder with 0.75 mm sieves to grind samples (Dietz Motoren KG, 1.1 KW, 2840 min)

Dry ice (Frozen CO_2)

Stainless steel pans (15 cm x 15 cm)

Forced draught oven

Desiccators

250 ml bottles with tight screw lids to store the samples in to minimize water absorption.

Step 1/1.4: Use the commercial meat saw to cut the frozen mirror image carcass portion/food refusals (**see 1.1.3 and step 5/1.4**) into pieces that can fit into a carcass grinder.

Step 2/1.4: Weigh and record mass **A** of food refusals/ mirror image carcass portion before each grinding.

Step 3/1.4: Grind the mirror image carcass portion/food refusals once through the Wolf grinder.

Step 4/1.4: Use the scraper to transfer all the ground meat to a bag. Weigh and record mass **B**. Freeze at –10°C.

Step 5/1.4: Repeat **step 3/1.4** and mix thoroughly.

Step 6/1.4: Use the scraper to transfer all the ground meat to a bag. Weigh and record the mass **C**.

Step 7/1.4: Mix the ground mirror image carcass portion/food refusals thoroughly and take a representative sample and freeze at -10°C. The sample must weigh approximately 400 g to provide enough DM for the chemical analysis.

Step 8/1.4: Determine correction factor to compensate moisture loss

$$\text{Total water loss (D)} = (A - C)$$

$$\text{Correction factor} = 1 - (D/A)$$

Step 9/1.4. Divide the sample into two stainless steel pans and dry at 100°C overnight.

Step 10/1.4: Mix the food refusals and mirror image carcass portion samples with dry ice on a 1:1 ratio (volume:volume) to prevent the fat from smearing during the grinding process.

Step 11/1.4: Grind the frozen food refusals/mirror image carcass portion sample through 0.75 mm sieves, mix thoroughly and store in 250 ml bottle.

1.5 Techniques for the chemical analysis of faeces, food refusal and mirror image carcass portion samples

1.5.1 Dry matter of food refusals/ mirror image carcass portion (DM)

Determine the DM_1 (see 1.3)

Determine the corrected DM_2:

$DM_2 = DM_1 * CF$

CF=Correction factor (see step 7/1.4)

1.5.1 Dry matter of faeces (see 1.3)

1.5.2 Crude Protein (CP)

Determine the CP content by using a Leco ® machine.

1.5.3 Lipid

Determine the lipid content using the hexane method in soxhlet apparatus (AOAC, 2000).

1.5.4 Gross Energy (GE)

Determine the GE by using an adiabatic bomb calorie meter (AOAC, 2000).

1.5.5 Minerals (ash)

Determine the minerals (ash) content by using a muffle furnace (AOAC, 2000).

1.6 Calculating digestibility

1.6.1 Apparent digestibility of DM

Apparent digestibility coefficient of DM = Intake-faeces/ intake (McDonald *et al.*, 1995)

Intake= Mass of diet/ration (DM) – mass of food refusals (DM).

1.6.2 Apparent digestibility of CP, fat, minerals (ash) and gross energy (GE)

Apparent digestibility coefficient of CP = CP in Intake - CP in faeces/ CP intake

CP in intake= CP in diet/ration fed – CP in food refusals.

The same will be done to determine apparent digestibility of fat, NFE, minerals (ash) and GE.