Digestibility studies with captive African lions (*Panthera leo*) fed unprocessed donkey carcasses – a proposed method

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Digestibility studies with captive African lions (*Panthera leo*) fed unprocessed donkey carcasses – a proposed method[1]

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Abstract
Apparent digestibility coefficients of unprocessed animal carcass diets were determined with captive African lions (*Panthera leo*) in the Bloemfontein Zoological Gardens. Procedures were developed to conduct digestibility trials with an adult male and a female lion, each comprising three replications in succession per lion. The diets comprised the unprocessed hind limbs or carcass portions of donkeys (*Equus asinus*). A carcass portion or 'trial diet', namely one of the two symmetrical hind limbs of a donkey, was fed to a specific lion and the other hind limb, the 'mirror image carcass portion' was retained and frozen pending analysis. Faeces excreted and food refused were collected, processed, frozen and stored pending analysis. Mean dry matter (DM) intake was 4.493 kg and 4.324 kg respectively for the male and female lion, with mean apparent DM digestibility coefficients of 0.854 and 0.902. The apparent digestibility coefficients for crude protein (CP), lipids and gross energy (GE) were 0.919 and 0.947; 0.995 and 0.993; 0.930 and 0.941, respectively for the two lions. The apparent digestibility coefficients for minerals were relatively low, respectively 0.310 and 0.528 for the male and female lions. Apparent digestibility coefficients for food, expressed as DM, can be useful to estimate the food and nutrient intake of large African predators. Evaluating the nutritional status of free-ranging large African predators might be possible in a non-invasive manner.

Key words: *Panthera leo*, digestibility, non-invasive techniques

Introduction

There is a paucity of information on quantitative nutritional aspects of African lions (*Panthera leo*), especially the digestion of diets by large African felids (Morris *et al*., 1974; Barbiers *et al*., 1982). Except these reports, little is available on the digestion of diets and absorption of nutrients by large African predators for conditions that closely resemble free-ranging feeding scenarios.

Free-ranging lions do not consume food daily and have access to unprocessed animal carcasses only, thus trial procedures were designed for captive lions to mimic the feeding conditions of free-ranging lions.

Being feast-and-famine feeders, lions ingest large quantities of food during meals, devouring skin, meat, and viscera; thus, almost everything is ingested except the large bones, hooves, skulls, and stomach contents of prey (Schaller, 1969). Lions can go for long periods without food, but when the opportunity avails, they consume large quantities of meat (Eloff, 1973a). The estimated daily food intake of lions varies between 4.7 and 14 kg and may exceed 40 kg or 25% of their own body mass (Schaller, 1969; 1972; Eloff, 1973a; Van Orsdol, 1982; Clark, 1987; Packer *et al*., 1990; Stander, 1992; Mills & Biggs, 1993). Food intake of lions varies with season and prey availability (Van Orsdol, 1982; Viljoen, 1993), but Packer *et al*. (1990)

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estimated a daily food requirement of 5 to 8.5 kg for survival and stated that male lions ingest twice as much food as females when feeding on the same carcass.

It is important to note that when food ingested is expressed as the daily food intake it may imply that lions eat every day, which is not the case. The feeding interval of lions varies considerably: 4 days was noted in the Kruger National Park, South Africa (Smuts, 1979) and 3.1 days in the Rwenzori National Park, Uganda (Van Orsdol, 1982). Similar feeding intervals were reported in the Serengeti National Park, Tanzania (Schaller, 1969). However, the feeding interval may be only one day (Bothma & Walker, 1999), while the maximum feeding interval observed in the Kruger National Park was 13 days (Smuts, 1979). It should be noted that in these reports the food intake of lions is invariably expressed on a fresh basis with diets of very high, but unknown, water content, further contributing to the variation.

The objective of this study was to develop non-invasive techniques to conduct digestibility trials with captive lions when consuming large unprocessed animal carcass portions that mimic the feeding processes of free-ranging large carnivores.

Material and methods

The study was conducted in the Bloemfontein Zoological Gardens (Bloemfontein Zoo) with an adult male and a female lion (Borstlap, 2002). The pair of lions were housed in a spacious facility consisting of two brick and concrete enclosed night chambers (2.35 m x 2.6 m and 5.65 m x 2.6 m), with steel grate trapdoors leading to a large open-air leisure yard. The trapdoors are remotely controlled by a system of pulleys and cables. The leisure yard measured 729 m^2 and the ground is mostly covered with Kikuyu grass (*Pennisetum clandestinum*), landscaped with a few large rocks and tree trunks, and a shallow water pond.

Two digestibility trials (Trial 1 and Trial 2), each comprising three replications in succession per lion (Replications 1, 2 and 3 each per trial), were performed as detailed in Table 1.

Table 1. The schedule of digestibility trials conducted with the captive male and female African lions, being fed large portions of unprocessed donkey carcasses.

Trial	Predator	Replication	Date
1	Male lion	1	27 February 2002
		2	4 March 2002
		3	22 May 2002
2	Female lion	1	29 May 2002
		2	5 June 2002
		3	9 June 2002

The lions were weighed in a non-invasive manner. A steel grid was placed on top of the two metal beams containing the pressure cells of an electronic cattle scale and positioned in the leisure yard, in front of the trapdoor leading to the night chambers. When the steel grid was placed in the leisure yard, the lions were uneasy and wary towards the foreign object; therefore, the lions were allowed a few days to get used to its presence before an attempt was made to weigh them. After zeroing the scale, a lion was lured with food onto the steel grid and the weight recorded. Every effort was made to avoid unnecessary disturbances and stress and the lions were not weighed while a digestibility trial was underway. The lions were weighed before being fed to reduce fluctuations in body weight due to gut fill.

The lions in the Bloemfontein Zoo were routinely fed large portions of food twice a week to mimic the feeding regime of free-ranging lions and the digestibility studies reported here were conducted with a minimum change in their customary feeding routines.

Specific procedures were developed to feed a large section of an unprocessed animal carcass to a lion and, very important, obtain homogenous representative samples from the same carcass for analysis (Figure 1). The diets consisted of two symmetrical portions of donkey carcasses that were divided into paired sections, *e.g.* the two hind limbs of a carcass. Lions have a destructive feeding habit; therefore, one limb section was fed to a specific lion ('trial diet') and the other symmetrical limb section ('mirror image carcass portion') was retained for analysis. It was assumed the mirror image carcass portion retained in each trial was identical in nutrient composition to the corresponding symmetrical trial diet offered to a lion.

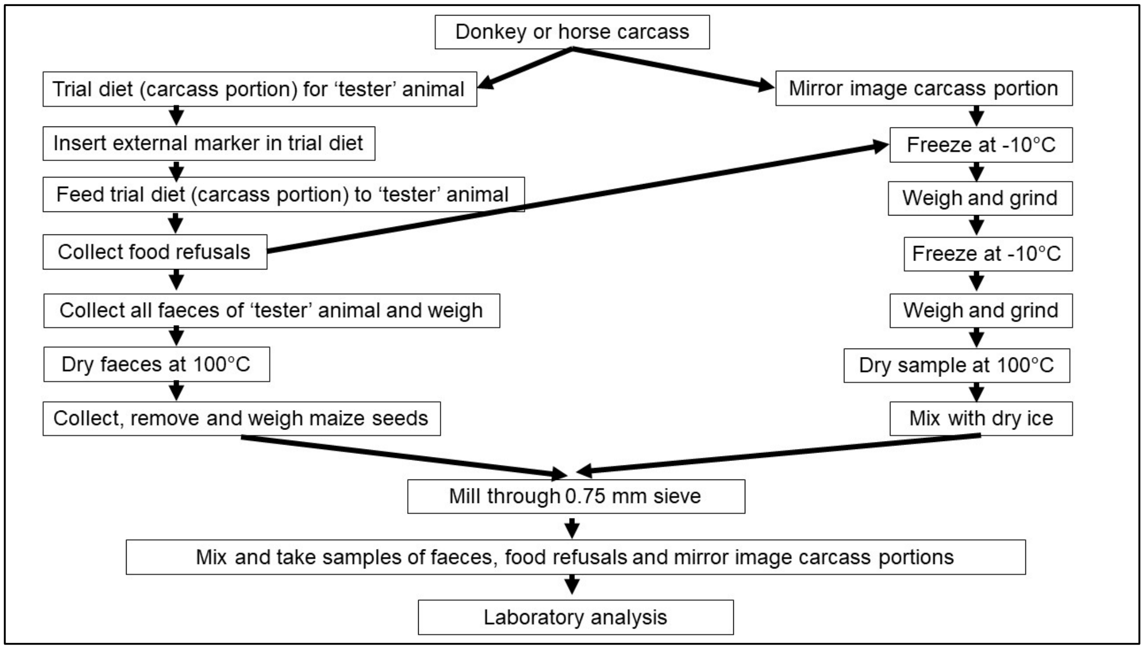

Figure 1 A schematic presentation of the experimental procedures followed in determining the food intake and digestibility trials with large African predators (Borstlap, 2002).

The donkeys were humanely harvested on a nearby farm with a silenced rifle and transported to the Bloemfontein Zoo. After eviscerating, but not skinning the donkey carcasses, the hind limbs were severed by cutting between the last lumbar and first sacral vertebrae before the pelvis. A butcher's meat saw was used to cut through the length of the sacral vertebrae to separate the two hindquarters, thus yielding two mirror images of a hindquarter each. The lower part or the hind leg was removed by cutting through the heel joint just below the tibia above the tarsus. The trial diet and corresponding mirror image carcass portion were weighed on a large platform scale. The mirror image carcass portions were sealed in large plastic bags, frozen and stored at -10°C pending further processing and analysis.

The pair of lions shared facilities in the Bloemfontein Zoo; therefore, an additional method of identification with an external marker was used to lace or mark the faeces of one individual. Thirty yellow maize (*Zea mays*) seeds were inserted into each trial diet before being offered to a lion ("tester" lion). Furthermore, the lion ("filler" lion) that was not participating in that specific digestibility trial was fed either chicken tripe or part of a skinned donkey ribcage. The dual system of identification made it easy to distinguish between the faeces of the lions.

Before feeding commenced between 14h00 and 15h00, the two lions were lured into separate night chambers and closed behind trapdoors. The leisure yard was inspected and all faeces, food refusals and bone remaining from previous meals removed.

The “filler” lion’s food (skinned donkey ribcage or chicken tripe) was placed in the leisure yard, the service gate closed remotely and locked. The trial diet, marked in advance with 30 maize seeds, was then placed in a vacant night chamber and after closing and locking the gate, the ”tester” lion was allowed to start feeding on the trial diet and the time recorded. The “filler” lion was then released back into the leisure yard to start feeding on its meal. The “tester” lion stayed overnight in its night chamber to allow it to consume as much of the trial diet as possible and to prevent the "filler' lion from feeding on the trial diet. This prolonged separation of the lions while feeding was the only deviation in the trial routine from the usual feeding routine practiced in the Bloemfontein Zoo.

The next morning, any remains of the trial diet that was not consumed (food refusals) was collected, sealed in plastic bags, weighed, frozen and stored at -10°C pending further processing.

All faeces excreted by the "tester" lion were collected from early in the morning the day after the trial diet was consumed. The time of faecal collection was recorded. Inspections for freshly voided faeces were made at 3-hour intervals during daylight only to minimise disturbance of the lions. The faeces were picked up with a large metal spatula, sealed in airtight plastic bags, weighed, frozen and stored at -10°C. Visible contamination of faeces with grass, twigs and soil were removed before weighing. Only faeces of the "tester" lion originating from the trial diet were collected. Faeces originating from a specific trial diet were usually excreted within 48 to 72 hours from offering the meal.

The frozen mirror image carcass portions and food refusals from the trial diets were taken from cold storage, cut into smaller pieces with a butcher’s meat saw (to fit in the holding chamber of an animal carcass grinder) and then kept frozen again. The smaller frozen carcass pieces were removed one by one from the freezer and ground through a heavy duty, animal carcass grinder. The 64 circular grinder blades produced considerable heat (friction) during the process of grinding the frozen carcass pieces, comprising flesh, bone, skin, and hair and a substantial amount of water was lost in the form of visible water vapour or steam. This water loss was estimated by difference in weight to correct the DM content of the sample.

After thoroughly mixing the ground animal material (mirror image carcass portions and food refusals), representative samples were taken, weighed in duplicate on pre-weighed stainless-steel pans and dried at 100^{o}C for 16 hours in a force draught oven to determine the DM content.

Representative samples of the ground carcass material and food refusals were mixed in a ratio of 1:1 (v:v) with crushed dry ice (frozen CO_2) and ground through a 0.75 mm sieve in a conventional Wiley mill. The dry ice kept the samples very cold and prevented the fat from smearing too much during the grinding process. The ground samples were stored in plastic containers with screw-on lids at -10^{o}C pending analysis.

The faeces collected during a trial were dried separately on stainless steel trays at 100^{o}C for 16 hours in a force draught oven and the DM content determined. The maize seeds were removed and weighed, and the weight subtracted from the dry mass of the faeces. The dried faeces were ground through a 0.75 mm screen in a conventional Wiley mill, mixed and representative samples stored in plastic containers with screw-on lids pending analysis.

The CP content of samples 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 (McDonald *et al*., 2011). The lipid content of samples was determined in a Soxhlet apparatus, using the hexane method (AOAC, 2000). The mineral (ash) content of samples was determined on a DM basis by incinerating samples in duplicate in porcelain crucibles for 4 hours at 600ºC in a muffle furnace (AOAC, 2000). The gross energy (GE) of samples was determined on a DM basis with an adiabatic bomb calorimeter (dds CP400 calorimeter by digital data systems c.c.) (AOAC, 2000).

In each trial, the nutrient composition of the food and the nutrient intake of the "tester" lion were determined by subtracting the total quantity (expressed in kg) of DM, CP, lipids, minerals and GE in the refusals from that contained in the mirror image carcass portions.

The apparent digestibility of food, or nutrients, is best defined as the proportion of ingested food, or nutrients, not excreted in the faeces and, therefore, assumed to be absorbed by the animal (McDonald *et al*., 2011) and calculated as follow:

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

Where intake (kg) = (kg food or nutrient presented) – (kg food or nutrient refused)

The descriptive statistics were generated using Proc Means (SAS, 1991).

Results

Given the difficulties of weighing dangerous large predators without being restrained or chemically immobilised, the lions were weighed once during this study. Using the non-invasive procedure described previously, the male weighed 188 kg and the lioness weighed 129 kg.

This trial was part of a larger study (Borstlap, 2002) and six large African predators (two lions, two leopards and two cheetahs) had to be weighed during the cause of the project. However, the two lions were also weighed occasionally in previous trials and in February 2001 the male and female weighed 182 kg and 137 kg, respectively; in May 2001 they weighed 171 kg and 121 kg, respectively. Given the feeding regime of large predators in the Bloemfontein Zoo, little changes in body mass were expected.

During the two digestibility trials (with three replicates each) with the two lions, most of the trial diets were consumed except for large bones and some connective tissue. In some cases, the epiphyses of the bones were also eaten. It was not an objective of this study, but if larger quantities of carcass were presented to the lions, their food intake could have been higher.

The composition of the donkey carcass portions fed to the two lions during the two digestibility trials, each comprising three replications per lion, is shown in Table 2.

Table 2. Nutrient composition and energy content of the donkey carcass portions[1] fed to the two captive African lions (*P. leo*) during the two trial periods.

Trial	Lion	Replication	Dry matter (DM) g/kg	Crude protein (CP) g/kg DM	Lipids g/kg DM	Minerals g/kg DM	Gross energy (GE) MJ/kg DM
1	male	1	380	609	222	171	22.720
		2	347	621	165	199	22.209
		3	337	577	271	142	25.184
2	female	1	295	655	184	156	23.778
		2	339	617	180	181	22.215
		3	445	539	288	143	24.145

[1] Based on the analysis of the six symmetrical "mirror image carcass portions" that was retained while the corresponding six carcass portions ("trial diets") were fed to the lions.

The feed intake, faeces excreted and apparent digestibility coefficients for the male and the female lions fed diets of unprocessed donkey carcass portions, expressed on a fresh and a DM basis respectively, are presented in Table 3 and Table 4.

Table 3. Fresh food intake, the faeces excreted and apparent digestibility coefficients of diets consisting of donkey carcass portions (expressed on a fresh, or as fed, basis) by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Fresh food intake kg	Fresh faeces excreted kg	Apparent digestibility coefficient	Replication	Fresh food intake kg	Fresh faeces excreted kg	Apparent 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

Table 4. Dry matter (DM) intake, faeces excreted and apparent DM digestibility coefficients of diets consisting of donkey carcass portions by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	DM intake kg	DM excreted kg	Apparent digestibility coefficient	Replication	DM intake kg	DM excreted kg	Apparent 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

The nutrient composition and energy content of the food ingested by the male and the female lions fed diets of unprocessed donkey carcass portions are presented in Table 5.

The CP, lipid, mineral and energy intake, faeces excreted and apparent digestibility coefficients for CP, lipids, mineral and energy by the male and the female lions fed diets of unprocessed donkey carcass portions are presented in Tables 6 to 9.

The nutrient composition and energy content of the faeces collected from the male and the female lions fed diets comprising large portions of unprocessed donkey carcass portions are presented in Table 10.

Table 5. The nutrient composition and energy content of the food ingested from diets consisting of donkey carcass portions by a male and female African lion.

Trial	Lion	Replication	Dry matter (DM) g/kg	Crude protein (CP) g/kg DM	Lipids g/kg DM	Minerals g/kg DM	Gross energy (GE) MJ/kg DM
1	Male	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	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

Table 6. The crude protein intake, faeces excreted and the apparent CP digestibility coefficients of diets consisting of donkey carcass portions by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Crude protein intake kg	Crude protein excreted kg	Apparent digestibility coefficient	Replication	Crude protein intake kg	Crude protein excreted kg	Apparent digestibility coefficient
1	3.502	0.240	0.931	1	2.850	0.236	0.917
2	2.335	0.179	0.923	2	2.176	0.112	0.949
3	2.850	0.284	0.900	3	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

The water intake derived from their diets by the male and the female lions fed unprocessed donkey carcass portions are presented in Table 11.

Discussion

As was expected, the six diets offered to the two lions differed in composition, especially the DM content. The smallest variation between diets was in their GE content.

The mean fresh food intake was 13.510 kg and 12.812 kg for the male and female lions respectively: constituting an intake of 7.2% and 9.9% of their respective body weights.

Three major challenges had to be addressed in developing the non-invasive procedures to conduct these digestibility trials with large African predators such as lions: (i) diets are consumed as unprocessed animal carcass portions and are heterogeneous in macroscopic (meat, bone, connective tissue, skin, and hair) and nutrient composition; (ii) different parts and varying quantities of the animal carcass diets are eaten; and (iii) most, or sometimes all food is consumed, leaving little or nothing to analyse. Furthermore, the parts not eaten, the so-called refusals, differ in composition from the original carcass portion that has been offered.

Table 7. The lipid intake, faeces excreted and the apparent lipid digestibility coefficients of diets consisting of donkey carcass portions by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Lipid intake kg	Lipid excreted kg	Apparent digestibility coefficient	Replication	Lipid intake kg	Lipid excreted kg	Apparent 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

Table 8. The mineral intake, faeces excreted and the apparent mineral digestibility coefficients of diets consisting of donkey carcass portions by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Mineral intake kg	Minerals excreted kg	Apparent digestibility coefficient	Replication	Mineral intake kg	Minerals excreted kg	Apparent 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[1]	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

[1] Corrected to zero – the high mineral content of the faeces relative to the mineral intake could only be ascribed to an undigested piece (or pieces) of bone from a previous meal that dislodged and was voided in the faeces during Replication 3 of Trial 1.

The apparent digestibility coefficients of the trial diets (expressed on a fresh basis) for the male and female lions were high, namely 0.889 and 0.929, respectively. The diets consisted of fresh animal carcass material with high water content, therefore a high apparent digestibility was to be expected.

The DM intake of the male was 4.493 kg and 4.324 kg for the lioness, with apparent DM digestibility coefficients of 0.854 and 0.902, respectively. It agrees with the 0.869 obtained with a sub-adult male lion fed the hindquarter of a female Red Hartebeest (*Alcelaphus buselaphus*) (H.O. de Waal and Yanna Smith 2001; unpublished data), but substantially higher than other reports. In this regard, Morris *et al*. (1974) and Barbiers *et al*. (1982) obtained apparent DM digestibility coefficients of 0.760 and 0.757 for male and female lions respectively using a minced meat-based commercial diet. An apparent DM digestibility coefficient of 0.946 was obtained with domestic cats (*Felis silvestris catus*), again on a diet of minced meat (Kendall *et al*., 1982).

Table 9. The gross energy (GE) intake, the GE of the faeces and the apparent GE digestibility coefficients of diets consisting of donkey carcass portions by a male and female African lion.

Trial 1				Trial 2			
Male lion				Female lion			
Replication	Gross energy intake MJ	Gross energy excreted MJ	Apparent digestibility coefficient	Replication	Gross energy intake MJ	Gross energy excreted MJ	Apparent 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

Table 10. The nutrient composition and energy content of the faeces collected from a male and female African lion fed unprocessed donkey carcass portions.

Trial	Lion	Replication	DM g/kg	Crude protein g/kg DM	Lipids g/kg DM	Minerals g/kg DM	Gross energy MJ/kg DM
1	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	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

Although the coefficients of variation (CV) were low in both instances, the CV's for DM intake were higher compared to those for the fresh food intake. This could be ascribed to the variation in DM content and composition of the trial diets. Therefore, food intake should be expressed as DM intake rather than as fresh food (or as fed) intake. Furthermore, expressing food intake by lions as a percentage of body mass is not feasible because it would entail more regular weighing of the predators; a procedure which is difficult, risky, and not practical. The small CV's for the apparent digestibility coefficients for both fresh and DM food intake suggest that there was a high measure of repeatability in the specific techniques applied in this study.

Comparing the composition of the animal material offered with that consumed, the DM and mineral content of the material consumed was lower, the CP content of the material consumed was higher, the lipid content of the material consumed was mostly lower, and the GE of the material consumed was higher than that offered.

Table 11. Water intake derived from the diets consisting of unprocessed donkey carcass portions by a male and female African lion.

Lion	Water intake derived from the trial diets kg	Water intake as a percentage of body weight %	Water intake per metabolic size $kg/kgW^{0.75}$
Male	9.017	4.8	0.178
Female	8.488	6.6	0.222

The high apparent CP digestibility coefficients of 0.919 and 0.947 show the efficiency at which a very important nutrient of carnivorous diets, namely protein, is digested by lions. Barbiers *et al*. (1982) fed a commercial minced meat-based diet and Morris *et al*. (1974) fed a venison-based diet to lions and reported respectively apparent CP digestibility coefficients of 0.831 and 0.888. In a study with domestic cats (*F. silvestris catus*) the apparent CP digestibility coefficient was 0.981 (Kendall *et al*., 1982). The high apparent digestibility coefficients of CP are very important in the nutrition of carnivores because protein is the main component of meat. Ammonia derived from amino acid catabolism in the liver is converted to urea and the urea excreted via the kidneys; the deaminated keto acids are converted to glucose in the liver and utilised as an energy source (McDonald *et al*., 2011). Protein thus provides the amino acid requirements of the large cats, as well as serving 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, animal fat in prey is usually consumed in smaller quantities than muscle and, therefore, is the second most important energy source of carnivores.

During the study, the lions ingested small amounts of green grass, which is common among carnivores. The grass ingested by free-ranging lions may at times be substantial and Smuts (1979) reported that a particular female ingested 200 g green grass. In this study, grass was ingested when little or no hair from the skin of the carcass portion was ingested or available to ingest. Hair and grass are relatively indigestible and, therefore, are of little nutritional importance to lions, but may act as natural laxatives to purge the digestive track of old and dead epithelial cells. However, the large quantities of indigestible donkey hair in the diets were excreted in the faeces of the lions and elevated its CP content, thus reducing the very high apparent CP digestibility coefficients.

Lions digest lipids to a very large extent as shown by the high apparent lipid digestibility coefficients of 0.995 and 0.993, respectively for the male and female lions. This is an important finding because lipids contain more energy than protein (McDonald *et al*., 2011). In this regard, Barbiers *et al*. (1982) reported a lipid digestibility coefficient of 0.947 for lions using a commercial meat-based diet, which is comparable to the results of this study, while Kendall *et al*. (1982) also reported a lipid digestibility coefficient of 0.957 for domestic cats. According to De Waal *et al*. (2004) the high fat content of lions' milk suggests a high dependency on dietary lipids even from birth.

According to Sinclair (1975, cited by Davidson *et al*. 1986), two species of Carnivora, the domestic cat (*F. silvestris catus*) and the African lion (*P. leo*) lack the ability to further desaturate the essential fatty acids, polyenoic, linoleic and α-linolenic. Therefore, these carnivores have 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*., 2011). A further positive implication of the high apparent digestibility coefficients of lipids is the potential for effective absorption of fat-soluble vitamins from the diets.

The apparent digestibility coefficients of the minerals are the lowest for all nutrients evaluated and show that lions do extract much minerals from animal matter, albeit not to a large extent. Furthermore, it was suspected that pieces of bone might have been retained temporarily in the digestive tract from a previous meal and after becoming dislodged again, were recovered in the faeces. Lions are feast-and-famine feeders, but the gastrointestinal tract is necessarily completely cleared of all indigestible animal matter after each meal. Bones, temporarily blackened by hydrochloric acid (HCl), have been retrieved from the glandular stomach of a lion (H.O. de Waal and W.J. Combrinck 2001; unpublished data), suggesting that bones may be trapped temporarily in the stomach before it passes down the intestines to be excreted.

The very high apparent GE digestibility coefficients show the ability of lions to extract energy containing nutrients from diets. The apparent GE digestibility coefficients of 0.930 and 0.941, respectively for the male and female lions, are higher than the 0.861 for lions fed a commercial meat-based diet (Barbiers *et al*., 1982), but more in line with the 0.950 reported by Kendall *et al*. (1982) for domestic cats. Lions are not very successful hunters and spend considerable energy during hunting to catch prey; thus, much of the energy derived from the diet is absorbed to compensate for the energy invested during hunting. The energy intake of carnivores varies according to the composition of the diet and body condition of the prey; hence, body condition of prey plays an important role in the energy status of predators.

The last faeces from a previous meal could be distinguished from the first faeces after offering the second meal as indicated by the presence of hair and a firmer texture compared to the softer, darker and relatively hair-free faeces marking the beginning of the next feeding's defecation. The first faeces after a meal were always darker in colour, softer in texture and free of hair, while the last faeces of a meal were always firmer and dryer and often also contained large quantities of hair if the lion ate a diet that contained hair. It was easy to identify the "filler" lion's faeces by several characteristics: faeces originating from chicken diets were lighter or paler in colour, while those from the donkey ribcage diet, where large quantities of bone were consumed, usually had a crumb-like texture and a whitish colour.

The composition of faeces excreted by the two lions during the digestibility trials show that it contained relatively little water, ranging in DM content from about 40 to 45%. The high CP content of the faeces is ascribed to indigestible hair originating from the carcass portions that passed through the digestive system; hair consists almost entirely of protein. The low lipid content of the faeces (less than 1% and 2% of faeces DM, respectively for the male and female lions; including small but unknown quantities secreted by the anal glands) shows how well lipids are digested and absorbed by lions. The high mineral content of the faeces is ascribed to pieces of bone passing through the digestive tract.

The faeces of lions are rough in texture and contain large amounts of hair and in some instances sand, seeds, leaves, feathers, grass and even porcupine quills (Eloff, 1999). The lions had no latrine or favourite place where they defecated in the leisure yard; the choice of a suitable place to defecate appeared to have been at random. The consistency of the faeces or scat changed over the periods after feeding when it was voided. The first scat voided had a lower DM content than faeces excreted later. The first scat was also darker in colour than the last collection. The dark colouration of the first scat may be due to the higher content of blood pigmentation relative to scats voided later. The shape of the scats also starts out as soft and pasty in texture changing to harder and "sausage" or cylindrical shapes. The last scat contained more hair and grass. The last scat excreted after a meal had a higher DM content and sometimes consisted mostly of hair. The practical implication 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 consistency or DM content and the shape of the different scats. The progressively higher DM content of the scat also suggests that the longer retention in the gastro-intestinal tract allowed for more water to be absorbed from the lower gut.

The water content may account for 85% of the total mass of prey animal bodies (Green *et al*., 1984). Therefore, lions may obtain sufficient water from blood and soft tissue of prey animals to meet a considerable part of their water requirements. Lions will, however, drink water regularly when it is available (Eloff, 1973b; 1980; 1999; Green *et al*., 1984; Bothma & Walker 1999). The data confirm that lions obtain a considerable amount of water from their diets. The large quantity of water retained by the lions relative to their metabolic size supports the observation (Owens & Owens, 1984) that even though they live in arid areas and 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 results of the digestibility trials with the African lions have shown that these obligate carnivores are well adapted to ingest and digest animal bodies. Although lions are adapted to a feast-and-famine lifestyle, they utilise their food and its nutrient content very efficiently.

Currently no method is available to directly determine the food intake of free-ranging large predators such as African lions. The procedures used in this study can assist in yielding estimates of the food and digestible nutrient intake of free-ranging lions. However, it remains a daunting challenge to observe and track a particular lion or several lions at close quarters to keep note of feedings and subsequent dropping of faeces, especially in some environments. All the faeces voided by a particular animal must be collected to increase the accuracy of estimating food and digestible nutrient intake. Due to the time interval it may take to collect fresh faeces excreted by a specific lion without risk and the varying rate at which water evaporates from the faeces until it is collected, the DM content of faeces should be used in estimating food intake.

If such information is available and the techniques described above applied judiciously and further refined, the food and nutrient intake of large African predators can be estimated. Thus, nutritional status of lions can be determined in a non-invasive manner during the different physiological stages of their lives.

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