GHENT UNIVERSITY
FACULTY OF VETERINARY MEDICINE
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Diet of the cheetah and function of its digestive system

Dhana Leemans

Promoters: Prof. dr. Geert Janssens
Dr. Laurie Marker

Literature Review
as part of the Master's Dissertation

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PREFACE

I first want to thank my promoter, Geert Janssens, to take the time to listen to my wildlife plans and wishes the first time I walked into his office. He gave me the chance to work with and write about my number one favourite animal.
I would also like to thank my friends, family and especially my husband for their support during my entire study of veterinary medicine and to help me bring about this literature study.

CONTENT

ABSTRACT

Over the past century, cheetah numbers in the wild have declined with 90% and the cheetah is listed on Appendix 1 by CITES, which include species threatened with extinction. It is therefore important to ensure the thriving and breeding of this species in captivity.

Studies show that this is not the case and that captive populations have a high prevalence of gastritis, glomerulosclerosis, systemic amyloidosis and veno-occlusive disease in comparison to free-ranging cheetahs. This suggests that properties of imprisonment are inducing factors in these disorders.

First, stress has a general negative influence on the function of an animal's immune system and can therefore play a role in any kind of disease. More specific, it is thought that stress plays an important part in the occurrence of glomerulosclerosis.

Secondary, choice of diet formulation can influence the prevalence of the degenerative diseases most frequently observed in this species. Carcasses exercise the masticatory apparatus, preventing the development of focal palatine erosion.
An excessive supply of protein increases production of several putrefactive compounds with negative effect especially on the kidneys plus, once amino acids are absorbed, they induce renal hypertension resulting in sclerosis.
Gastritis was also more common in animals fed horsemeat or had a high intake of crude protein and less common in animals fed chicken or hides, viscera, ribs, muscle meat at least once per week.

The goal is to improve feeding strategies to reduce the prevalence of these disorders linked to captive housing of cheetahs.

Key words: carcass, cheetah, gastritis, glomerulosclerosis, nutrition

SAMENVATTING

Tijdens de afgelopen eeuw zijn de aantallen van jachtluipaarden in het wild gedaald met 90%. De soort is ook opgenomen in appendix 1 van CITES, deze bevat de diersoorten die met uitsterven bedreigd zijn. Het is daarom belangrijk ervoor te zorgen dat deze diersoort het goed doet in gevangenschap.

De anatomie van de jachtluipaard verschilt in deze van andere grote katachtige. Hij kent aanpassingen die het mogelijk maken om snelheden tot 103km/u te bereiken. Door zijn slanke lichaam, kleine schedel en korte tanden geeft hij de voorkeur aan prooien tussen 23 en 56 kg. Mannelijke dieren vormen vaak coalities en zij zijn in staat grotere prooien neer te halen. Verder kan hij daardoor zichzelf ook niet verdedigen tegen andere roofdieren. Een jachtluipaard zal dan ook nooit te lang bij een prooi blijven om een mogelijke confrontatie te vermijden.

Uit gegevens verzameld van observaties in 6 landen over een tijdspanne van ongeveer 50 jaar blijkt dat enkele diersoorten frequenter worden gedood door jachtluipaarden. Dit impliceert dat jachtluipaarden de voorkeur geven aan deze soorten: Blesbok, impala, springbok, Thomson's gazelles en Grat's gazellen.

Een studie van 2013 geeft het dieet weer van 12% van de jachtluipaarden wereldwijd gehouden in gevangenschap. Het meest voorkomende dieet was rauw vlees (37%), gevolgde door commercieel bereide diëten (20%) en karkassen (8%). 35% van de jachtluipaarden krijgt een mengeling van deze diëten.

Het blijkt dat jachtluipaarden in gevangenschap een hogere prevalentie kennen van enkele degeneratieve ziekten in vergelijking met wilde jachtluipaarden van ongeveer dezelfde leeftijd. De populaties in gevangenschap had een hoge prevalentie van gastritis, glomerulosclerose, systemische amyloïdose en veno-occlusieve ziekte.

In de eerste plaats heeft stress een algemene negatieve invloed op de werking van het immuunsysteem en kan dus een rol spelen bij elke ziekte.
Verder is het type dieet een belangrijke factor. Karkassen oefenen het kauwapparaat, het voorkomt op die manier mee van de ontwikkeling van focal palatine erosion.
Een overmatige aanvoer van eiwit verhoogt de productie van verscheidene schadelijke verbindingen met een negatief effect in het bijzonder op de nieren plus, eenmaal de aminozuren geabsorbeerd zijn, induceren ze renale hypertensie en sclerose.
Gastritis komt ook vaker voor bij dieren die paardenvlees of een hoge inname van ruw eiwit kennen. Gastritis komt minder vaak voor bij dieren die minimaal één keer per week gevoed worden met kip, huiden, ingewanden of ribben.

Door voederstrategieën te verbeteren kan de prevalentie van deze aandoeningen in gevangenschap teruggedrongen worden.

Katachtige hebben een relatief klein colon, met een lengte van ongeveer 20% van de totale lengte van het spijsverteringskanaal. In het colon maar bij katten ook in de dunne darmen is een intestinale microbiota aanwezig. Deze lijkt bij jachtluipaarden in gevangenschap redelijk stabiel te zijn. Een studie over 3 jaar toonde ongeveer 24% verandering tussen opeenvolgende monsters in gezonde jachtluipaarden. De microbiota wordt voornamelijk gedomineerd door leden van Clostridium clusters en Lactobacillaceae.

Uit fermentatie van eiwitten en koolhydraten kunnen voedzame componenten gevormd worden maar ook schadelijke. Uit recent onderzoek blijkt dat bij jachtluipaarden die karkassen eten de concentraties van indoxyl sulfaat in het bloed dalen. De aanwezigheid van minder goed verteerbare vezels in het dieet heeft blijkbaar een positieve invloed.

Katten hebben essentiële voedingsstoffen die niet essentieel zijn in andere zoogdieren. Het is aannemelijk dat door het hoge eiwitgehalte in hun voeding sommige enzymen zijn verdwenen of gewijzigd. Deze verschillen in enzymen leiden normaal gesproken niet tot tekorten in gezonde katten die een verse, natuurlijke voeding krijgen.

INTRODUCTION

The purpose of this literature review is to integrate all existing information about the diet of the cheetah. To understand what kind of prey the cheetah prefers, information about anatomical limitations and hunting strategies were included, as well as data from feeding strategies in a captive setting.

This literature review provides an overview of diet-associated illnesses. To understand the link between diet and pathology, form and function of the gastro-intestinal tract and its microorganisms have been addressed. The goal is to improve feeding strategies and to address diseases that may result from poor nutrition.

The cheetah was first classified as *Felis jubatus* but when realizing that the cheetah was unique in different ways from other cats the genus was changed into *Acinonyx*. The cheetah is the only surviving species in that genus. In Greek, *Acinonyx jubatus* is a reference to the species-specific form of their claws. (Marker, 2002)

Over the past century, cheetah numbers in the wild have declined with 90%. In protected areas, numbers of competitive predators such as leopards and lions can become high whereby cheetahs immigrate into non-protected areas. Furthermore, the habitat of the cheetah is lost to human population and prey numbers decline. (Marker, 2002)
Today, wild cheetahs can be found in two continents. In Asia, in Iran and possibly Pakistan, approximately 100 cheetahs inhabit a small region. In Africa, less than 15000 cheetahs exist dispersed over an area covering 29 countries. (Marker, 2002)
Another factor to consider is that the cheetah is a genetically uniform species. The genetic monomorphism at examined loci in the cheetah is almost non-existent in other wild species. Such genetic uniformity might have resulted from a population bottleneck followed by inbreeding. (O'Brien et al, 1985) The bottleneck is placed at the end of the Pleistocene, when major extinction of large vertebrates occurred, about 10000 years ago. This was determined by back calculation of the divergence of mtDNA in Felidae and mutation rates of VNTR loci in other species. (Menotti-Raymond et al, 1992) The lack of genetic variation has several consequences. This could be the cause of reproductive abnormalities seen in this species. Spermatozoa concentration, percent mobility and normal morphology are less than that observed in domestic cats. (Wildt et al, 1983) There is a correlation between the reduction in genetic diversity with skeletal and congenital abnormalities (Marker-Kraus, 1997). This may also influence the immune system. For example, a much higher percentage of the cheetah population has succumbed to FIPV than in the domestic cat population. This may be due in part to an abnormality in their immune response. (Evermann et al, 1989)
Because of the inability to express deleterious recessive alleles the cheetah is more susceptible to environmental and ecological changes (O'Brien et al, 1985).

The cheetah is listed on Appendix 1 by CITES. Cites, the convention on international trade in endangered species of wild fauna and flora, wants to ensure that harvesting and international trade does not threaten the survival of species. Over different appendices they classify species depending on the level of protection they need. Appendix 1 catalogues species that are the most endangered among CITES-listed animals and plants.

LITERATURE STUDY

1. DIET OF THE CHEETAH

1.1 CHEETAH ANATOMY: BUILT FOR SPEED AND ITS CONSEQUENCES

The cheetah's hunting strategy is a combination of stalking and a high-speed pursuit (Hilborn et al, 2012). During the pursuit, the cheetah can reach a speed of 103 km/h making it the fastest land mammal in the world (Sharp et al, 1996). This way of hunting has been made possible through special morphological and physiological adaptations (O'Brien et al, 1983).

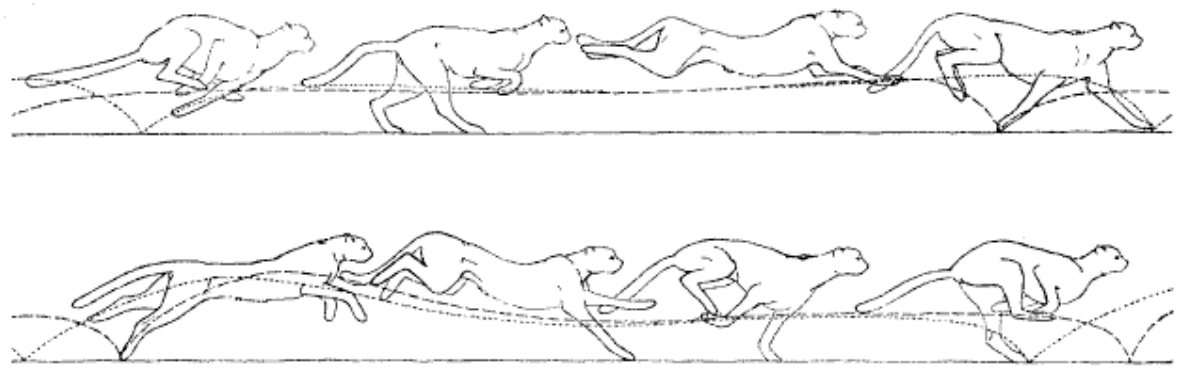

*Fig. 1: cheetah running at 90km/h (*Hildebrand, 1961)

To ensure sufficient oxygen delivery, cheetahs are endowed with a powerful heart and strong arteries combined with enlarged lungs and bronchi (Hunter et al, 2004; Marker, 2002).

The legs are slender and the most elongated of any large cat. The relative lengths of radius and humerus are identical and the scapula is longer than in any other cat species. (Ewer, 1973; Hunter et al, 2003) The scapula's inner surface for attachment of the levator scapulae and serratus muscles is deep and narrow. This is necessary because muscles in cursorial species work at different angels from climbing species. (Ewer, 1973) The lower parts of the leg are free of muscle mass, which is concentrated higher up on the limb and close to the body. The bones of the paws are light and thin. To restrict rotation while sprinting, the bones are firmly bound together with strong ligaments. (Hunter et al, 2003) The fibula is long and slender and is closely bound to the tibia by fibrous tissue (Ewer, 1973).

The muscles in forelimb and hind limb differ to comply with the differences in function of the legs. The forelimb mainly has Type I fibres in contrast to the hind limb, which mainly has Type II. This is because the propelling action arises from the hind limb. (Goto et al, 2012)

The spine especially affects the stride length and cheetahs have proportionally the longest one of all cats (Hildebrand, 1961). Together with a high percentage of type II muscle fibres in the longissimus the cheetah can run at about 1 stride per 0,28 seconds (Goto et al, 2012; Marker, 2002).

As previously mentioned, the legs of cheetahs are adapted to running at high speed; therefore they can only partially retract their claws. They also lack the protective sheath of skin that houses the claws. Fully extended during a chase, they provide extra traction. The dewclaw is different; it is not straight as all other claws but curved. The dewclaw does have a sheath of skin and is retractable. Its function is bringing down prey. Because the other claws are tooled for speed, this claw tackles prey and does the work that all claws of the foreleg normally do in other cats. In order to obtain even more traction, the pads of the feet have longitudinal ridges. (Ewer, 1973; Hunter et al, 2003; Russell et al, 2000)

The canines of a cheetah are small and thus the roots are small, creating space for an enlarged nasal passage. This way, more air can be sucked in during exercise or while holding the prey by the throat. (Ewer, 1973) The skull is small; the jaws are short and can therefore not support a large masseter muscle (Marker et al, 2003).

Fig.2: A cheetah and its small skull, short jaws and small teeth, foto by Dhana Leemans

With claws shaped for traction, small teeth and slender legs the cheetah easily looses its prey to kleptoparasites. Up to 12% of kills can be lost to kleptoparasites, spotted hyena and lion in particular. To minimize the chance of a confrontation with these predators, the cheetah is diurnal. (Hayward et al, 2006; Marker et al, 2003)
This also results in a shorter time spent at a kill when there is a high density of competing predators in the area (Mills et al, 2004).

Because of the smaller skull and teeth, the cheetah is incapable of crushing thick bones. A cheetah will eat the bones of a newborn but only the thinner bones of an adult. (Ewer, 1973; Phillips, 1993) Furthermore cheetahs will often kill prey with a body weight less than their own. This is probably also a result of the fact that these cats cannot manipulate their prey with their forelimbs. (Russell et al, 2000) The cheetah uses the throat bite to kill its prey most frequently of all large cats. Because of the relatively short canines the neck bite has been replaced by the throat bite for all except the smallest prey. (Ewer, 1973)

1.2 HUNTING STRATEGIES AND PREY SELECTION

1.2.1 Making a kill

Cheetahs are carnivorous animals that hunt alone or occasionally in small groups. These small groups are coalitions of males. Coalitions have some advantages over solitary animals such as better access to females for breeding and better defence of their territory. (Marker, 2002) Cheetahs inhabit different habitats and make slight adaptations to their hunting strategy depending on the presence of cover. In wooded habitats they can approach prey more easily which makes the chase distance shorter but obstructs high-speed hunting. A plus is that in wooded habitats, kleptoparasites have more difficulties spotting a cheetah and its kill. Nevertheless, cheetahs in all types of habitats seem to prefer open grassland for hunting. (Mills et al, 2004) Coalitions of males hunt together but do not really work together. During a hunt, the other cheetahs may prevent an adult from defending their youngster or help bringing down a large animal but that is all for collaboration. (Hunter et al, 2003) A study in Tanzania showed that single cheetahs had to undertake more hunts to get the same number of kills as a coalition and a coalition of two seemed to be the most efficient (Randall, 1970).

Fig. 3: coalition of two males, resting in the shade, foto by Dhana Leemans

At the start a chase, the cheetah is, in most cases, further from its target than other cats. A cheetah can run at full speed for about 500m. Due to his high speed, he usually overtakes his prey within 200-300m. When he reaches the prey he plants his dewclaw in the animal's hind leg. At the same time, the cheetah shifts his weight causing the prey to lose balance and trip. Than the cheetah bites the animal in the ventral region of the neck, causing death by strangulation. (Russell et al, 2000)

The cheetah utilizes different hunting strategies modified to specific situations. The most common way of hunting is to stalk as near to the prey as possible. When the cheetah can get within striking distance he will launch an attack directed at the selected animal. A different method often used when there is a lack of cover is one where the cheetah walks towards a herd. The animals in the herd are aware of his presence. If the cheetah can get within 70m of an animal within the herd before they run away, the cheetah will attack. Another strategy is running full speed towards an unsuspecting herd, trying to get in striking distance before they take off. Finally, the cheetah sometimes sits and waits until a herd moves close enough towards his position. (Rich et al, 2004)

Different situations can influence the cheetah to start a chase or not. The decision to hunt is stimulated by the presence of prey. Satiated cheetahs still engage in stalks and chases so hunger is not a decisive factor. This factor was examined by comparing belly size with the probability of hunting. According to Caro 1994, belly size reflects the hunger level of cheetahs. In contrast, the decision is adversely affected by the presence of competitors such as lions. (Cooper et al, 2006)

Once a kill has been made, the cheetah will start consuming his prize. They will first feed on the organs, except for the intestines. Aside from organs, muscle tissue is consumed but the appendicular musculature remains untouched at many kills. If the prey weighs less than 10 kg, all bones will probably be consumed except for the skull. If the prey is larger, between 30-50 kg, only parts of the rib cage and vertebral column will be consumed. Cheetahs can consume up to 10 kg of food in 2 hours. In most cases they will leave their kill after 1 or 2 hours to avoid encounters with stronger predators. When the population of lions and hyenas in the area is low, they can stay at a kill for a longer period of time. (Phillips, 1993)
Studies at Kruger National Park show that cheetahs in a coalition obtain about 1.4 kg/d/cheetah (Mills et al, 2004).

Several factors have an influence on hunting success. The older the cheetah, the more he succeeds in finishing a chase with a kill. Hunting is a learnt behaviour so it takes time for youngsters to optimise their skills. The prey detects sub-adults more frequently during the stalk than adults and sub-adults will often still start a chase after being discovered. (Hilborn et al, 2012)
Hunting success declines as quarry herds contain more animals. Large herds detect predators from a greater distance wherefore the animals can respond accordingly. Furthermore, a large number of fleeing animals make it difficult for a predator to focus on one animal. (Fitzgibbon, 1989)
Finally, as prey size goes down, hunting success increases (Hilborn et al, 2012).

1.2.2 Prey selection

When approaching a herd of gazelles, the cheetah will focus his effort on the least vigilant animals. The chances of making a kill are higher because for one, less vigilant animals are likely to react more slowly when the cheetah unleashes his attack. Secondly, less vigilant animals can be in poor physical condition. To maximize their energy intake, they spend more time feeding, not keeping an eye on their surroundings. (Fitzgibbon, 1988)
As previously mentioned, the cheetah's anatomical adaptations make him the fasted land mammal in the world, which has implications on prey selection. Because of their slender body, small skull and small teeth, the cheetah prefers prey within a range of 23-56 kg. (Hayward et al, 2006) Male coalitions can bring down slightly bigger prey because they work together while bringing the animal down (Mills et al, 2004).

Data compiled from six countries: Kenya, Namibia, South-Africa, Tanzania, Zambia and Zimbabwe over a time span starting from 1956 till 2005 shows five prey species that are killed more frequently than expected based on their abundance. This implicates that cheetahs prefer these species: blesbok, impala, springbok, Thomson's gazelles and Grat's gazelles. (Hayward et al, 2006)
Small prey might be underrepresented because most of these studies use data from observations of a kill or finding carcass remains. Kills of small prey are often unobserved because of quick consumption and lack of remains (Randall, 1970).

Fig. 4: mother and cub feeding on a springbok, foto by Vicky Morey Van Roost

The Thomson's gazelle is the cheetah's preferred prey species in the Serengeti plains. This might be influenced by the high numbers of this species in that specific area. It is even more pronounced during breeding season when almost every chase of a Thomson's gazelle fawns ends in a kill. (Hayward et al, 2006)
Another observation was that more male gazelles were killed than expected from the sex ratio in that area. First, male Thomson's gazelles spend more time at the periphery of the groups in comparison with females. Secondly, males weigh approximately 20% more than females. Cheetahs would only prefer females if hunting success rates were much higher to compensate for the 20% difference in energy. Thirdly, male Thomson's gazelles seem to be more susceptible to sarcoptic mange. If infection is severe it can result in lesser fitness, which makes them easy prey. (Hayward, 1989)

1.3 FEEDING CAPTIVE CHEETAHS

1.3.1 The diet

It is understandable that organisations that house cheetahs in captivity cannot recreate a completely natural existence. A free ranging cheetah with an average litter of three cubs spends 40% of its time on satisfying nutritional requirements. This time is spent on locating, capturing and killing quarry and behaviour at a kill. During these actions, a cheetah uses appropriate body equipment such as teeth, jaws and claws. (Lindburg, 1988)

Adult male cheetahs averaging 40 kg require 9.21 MJ/day (maintenance energy) and females averaging 30 require 7.54 MJ/day (Marker et al, 1998). Most zoos in North America feed their cheetahs a commercially prepared horsemeat-based mixture with additional carcasses (portions or whole) once or twice per week (Boler et al, 2009). On average, the cheetahs eat about 1.4 kg daily and little more than half of the zoos utilize a fasting day every week. This feeding schedule results in an intake of approximately 7,52 MJ per cheetah per day (Dierenfeld, 1993). At the Cheetah Conservation Fund in Namibia, global leader in research and conservation of cheetahs, adult cheetahs are fed carcass portions covered with a powder containing vitamins and minerals ranging from 1.4 to 1.6 kg per cheetah per day (personal observations). From these pieces most fat and the skin were removed. They were fasted once a week and got additional organ, about 500 g per cheetah when available.

Captive cheetahs that are fed supplemented pieces of meat do not seem to get a well-balanced calcium:phosphorus ratio. Whole rabbit carcasses for example provide a more complete source of minerals. (Depauw et al, 2011)

In the past, zoos have based themselves on diets of domestic cats to compose those of captive wild cats (Vester et al, 2009). Domesticated cats might have adapted to a diet with a higher carbohydrate

concentration in comparison to their wild ancestors. (Plantinga et al, 2011). Therefore it is important that zoos try to mimic the cheetah's natural diet and not rely on that of domestic cats.

A study carried out in 2013 reports the diet of 12% of the captive cheetah population housed in 33% facilities known to have cheetahs. The most common diet type was raw meat (37%), followed by commercially prepared food (20%) and carcasses (8%). A mixture of these diets was fed to 35%. Of these diets, 53% were supplemented with vitamins and minerals. (Whitehouse-Tedd et al, 2015)

Zoo visitors can object to seeing carnivores feeding on whole carcasses. Because zoos are financially dependent on their visitors, some zoos decided to switch from whole carcasses to pieces of meat or a commercial diet. (Young, 1997) It is therefore important to educate the public and zoos have a vital role in that process.

1.3.2 Consequences on health of the animals

Some disorders are more common in cheetahs in captivity than in the wild. This suggests that properties of captivity are inducing factors in these disorders. Because of the genetic monomorphism in the cheetah and lack of heterogeneity at the HCM loci, infectious diseases were presumed. Yet, a study showed that the causes of mortality in captive cheetahs are mostly degenerative diseases and there is a correlation between severity of the disease and time spent in captivity. This emphasizes even more the importance of the properties of imprisonment in the pathogenesis of these disorders. (Terio et al, 2003)

A study compared disease prevalence in free-ranging Namibian cheetahs with those in two captive populations of similar ages. The captive populations had a high prevalence of gastritis, glomerulosclerosis, systemic amyloidosis and veno-occlusive disease. (Munson et al, 2004)

	free-ranging Namibia	captive North America	captive South Africa
gastritis	11%	99%	99%
glomerulosclerosis	13%	67%	81%
renal amyloidosis	4%	35%	37%
veno-occlusive disease	9%	56%	93%
adrenal cortex hyperplasia	8%	63%	43%

Fig. 5: Disease prevalence in free-ranging Namibian cheetahs compared to captive populations (Munson et al, 2004)

A first property of imprisonment to address is the presence of stress in captive animals. Stress results in the release of ACTH, which stimulates cells of the adrenal cortex. The long-term result is a hyperplasia of the cortex, which has been observed in captive but not in free-ranging cheetahs. (Terio et al, 2003) Stress has a general negative influence on the function of an animal's immune system and

can therefore play a role in any kind of disease. More specific, it is thought that stress plays an important part in the occurrence of glomerulosclerosis. Renal lesions most closely resemble these of early diabetes mellitus. But since none of these animals had pancreatic lesions and no other symptoms of diabetes were present, the cause for this could be the exposure to chronic stress. 80% of the animals in the study had adrenocortical hyperpasia, which results in hyperglycemia and could explain the type of lesions in the kidneys. (Bolton et al, 1999)

The diet and the way in which it is offered can reduce the amount of stress experienced by the animal. Temporal and spatial variation in feeding reduces the occurrence of stereotypical behavior. Since the time spent pacing correlates with excreted levels of cortisol metabolites, the reduction of stereotypical behavior is an indication for stress reduction. By changing the feeding routine and making it less predictable, stress and its negative effects on health can be limited. (Quirke et al, 2011; Quirke et al, 2012) Not only time and place of food provision is important but also the form in which it is presented. Carcasses or portions of carcasses make cheetahs more possessive over their food, play is more often observed around the food and the animals take more time to smell. Longer time is spent on their food than cheetahs fed a formulated diet, making less time for boredom. (Bond et al, 1989; Lindburg, 1988)

A second property is the diet. In captivity, cheetahs can be fed commercial diets, raw meat, carcasses or a mixture of these. The choice of diet formulation can influence the prevalence of the degenerative diseases most frequently observed in this species.

When fed carcasses, the animals need to exercise their masticatory apparatus. Insufficient wear and atrophy from disuse of the masticatory apparatus contributes to the development of focal palatine erosion. This is a self-inflicted injury of the palate causes by the lower first molars. Food particles can be lodged in the defect and cause inflammation. This disorder has only been described in captive cheetahs fed a soft, commercial diet. (Fitch et al, 1982) Soft food also tends to produce more bacterial plaque than firm food (Egelberg, 1965). Firm food has a stimulating effect on the capillaries in the gingival tissue, which improves vitality of all of the supporting structures (Burwasser et al, 1939; Pelzer, 1940).

An excessive supply of protein can have several detrimental effects on the feline's health. Feeding too frequently or only providing skeletal meat can cause this excessive supply. When this surplus of protein reaches the large intestine microbial fermentation increases. Fermentation of protein leads among other things to the production of several putrefactive compounds such as ammonia, indole, phenol, p-cresol, and biogenic amines. (Depauw et al, 2012) Tyrosine and tryptophan are metabolized by colonic bacteria to respectively p-cresol and indole. Indole is metabolized in the liver to indoxyl sulphate and p-cresol is metabolized to p-cresyl sulphate in the intestinal membrane. Transported in the bloodstream, these protein metabolites have a negative effect on kidney function, inducing for example glomerular sclerosis, which could explain the high prevalence of glomerulosclerosis in

captive cheetahs. Other organ systems are affected as well resulting for example in aortic calcification and aortic wall thickening. (Niwa, 2010; Rossi et al, 2013) An additional effect of excessive protein absorption on the kidneys is the induction of increased renal blood flow and renal hypertension resulting in sclerosis (Bosch et al, 1983; Friedman, 2004).

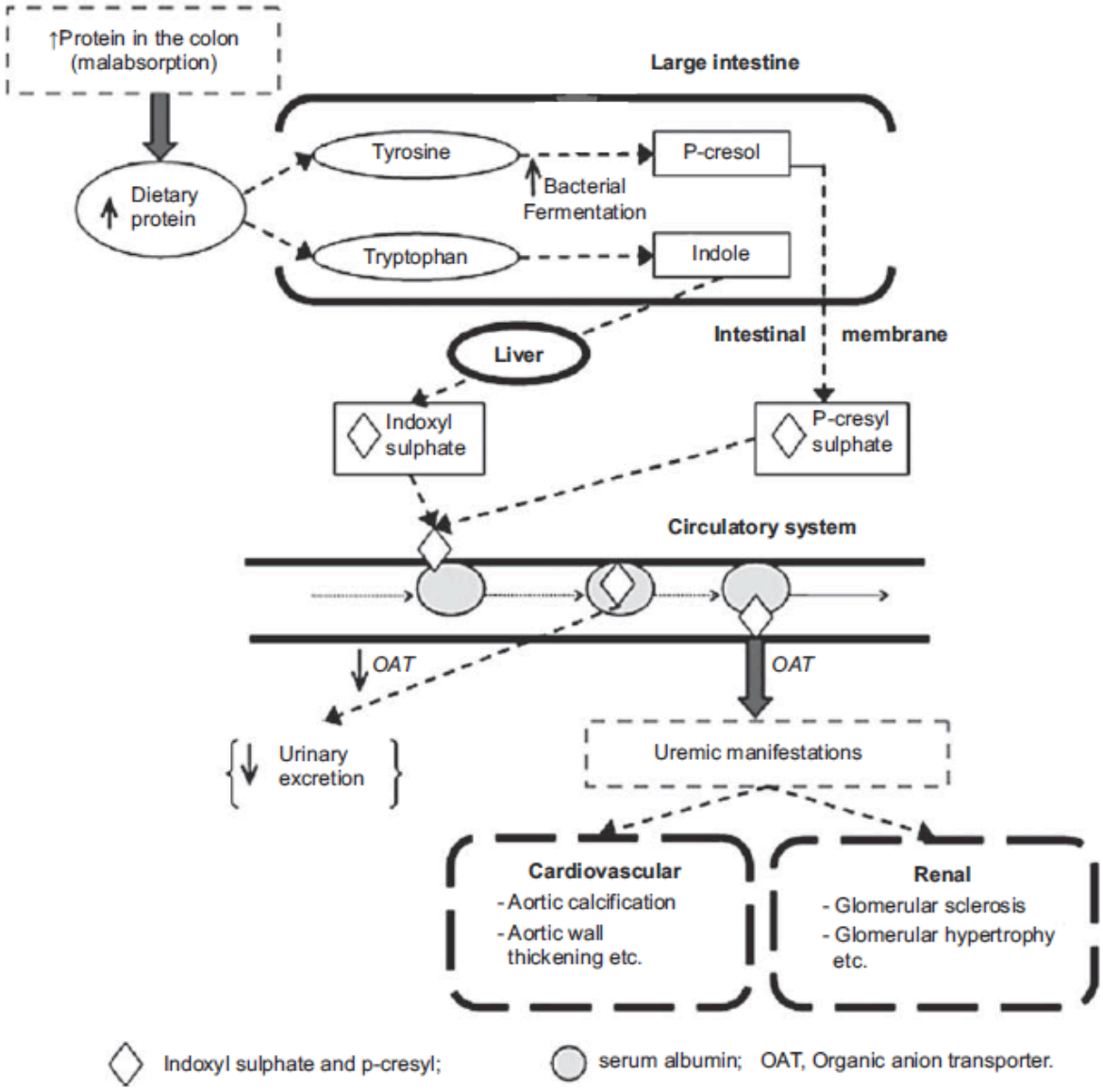

Fig. 6: Toxicokinetics of indoxyl sulphate and p-cresyl sulphate (Rossi et al, 2013)

56% of North American and 93% of South African captive cheetahs suffer from veno-occlusive disease (VOD) in comparison to 8% in a free-ranging population. In 70% of livers with these lesions, a proliferation of Ito cells was established. Hypervitaminosis A may be responsible since Ito cells are vitamin A storing cells. These cells are found in the perisinusoidal space resulting in a perisinusoidal fibrosis that could possibly evolve into VOD. (Gosselin et al, 1988) Food with a high content of vitamin A, liver for example or to much vitamin supplementation could be an inducer of this disease in a captive setting.

A survey conducted in 2013 including 184 captive cheetahs in 86 international facilities compared the prevalence of certain diseases to type of diet. This survey demonstrated that animals suffer less from diarrhea when their diet includes carcasses or ribs at least once per week. Animals would vomit less frequent when fed long bones at least once every weak and would vomit more frequent when fed goat meat. Gastritis was also more common in animals fed horsemeat or had a high intake of crude protein. Both goat and horse meat have a high protein content. This protein excess can modify microbiota composition and increase the production of putrefactive compounds. Gastritis was less common in animals fed chicken or hides, viscera, ribs, muscle meat at least once per week. (Whitehouse-Tedd et al, 2015)

An explanation for the high prevalence of systemic AA amyloidosis and renal amyloidosis is the high prevalence of gastritis in the cheetahs. In 100% of the cheetahs with renal amyloidosis, an inflammation disease was identified, most commonly gastritis. (Papendick et al, 1997) Serum amyloid A protein, a serum precursor of AA-protein is produced in a variety of conditions such as inflammation. The amyloid deposits in organs and impairs normal organ function.
(Kumon et al., 1993)

2. THE DIGESTIVE SYSTEM

2.1 FORM AND FUNCTION

Felines have well developed non-gustatory papillae on the dorsal surface of their tongues. These sharp, hard, backwardly directed papillae help removing meat from bones while feeding. The oesophagus in carnivores has striated muscle extends all the way to the stomach which makes it possible for them to regurgitate easily. (Ewer, 1973)
Felidae usually have 30 teeth in their permanent dentition: 6 incisors, 2 canines, 6 premolars and 2 molars in the maxilla; 6 incisors, 2 canines, 4 premolars and 2 molars in the mandible. P2 is regularly absent in cheetahs as in a number of other short-faced species as the caracal, lynx, etc. (Ewer, 1973). In cheetahs the cheek teeth are very narrow and together with the small roots incapable of dealing with large bones.

Carnivores and especially felines have a simple stomach, a predominant small intestinal tract and diminished large intestinal tract with a reduction in the distinction between colon and rectum. Felines have a relatively small colon, its length is only about 20% of the total length of their digestive tract. (Ewer, 1973; Kerr et al, 2013)
Most components are absorbed in the small intestine (Stevens et al, 2004). The wall of the small intestine has villi to enlarge its surface and maximise absorption. In the small intestine, the duodenum is a mixing site and absorption mainly takes place in the jejunum. Monosaccharides, amino acids and peptides are actively absorbed. Carrier proteins transfer these nutrients across the intestinal wall. Fats

are absorbed by passive diffusion after micelle formation. Short-chain fatty aids (SCFA) are absorbed in the bloodstream without the need for bile salts. Minerals and water-soluble vitamins are absorbed by diffusion and carrier-mediated transport. Fat-soluble vitamins (vitamin A, D, E and K) are transferred across the brush border by passive diffusion. (McDonald et al, 2011)
Digesta have higher oxygen content and move at a higher velocity in the proximal part of the digestive tract. When the content reaches the large intestine, there is no more oxygen present and bacteria commence fermentation. (Buddington et al, 1998)

2.2 INTESTINAL MICROBIOTA

The intestinal tract is sterile at birth. Through the ingestion of food, microorganisms enter the digestive tract. Cats, unlike other mammals, have a high number of bacteria in the proximal part of their small intestine. (Papasouliotis et al, 1998) The presence of a microbial flora in the intestines has several advantages. They compete with pathogenic microorganisms for nutrients and adhesion sites. The normal microbiota can break down food components so the host can use them. This also lets the host adapt more easily to dietary changes. They can produce new components, which can serve as a source of energy or influence the host's gastrointestinal function. (Hooper et al, 2002) The latter shows that bacteria itself can influence function of the host's digestive tract. In dogs, glucagon-like peptides 1 and 2 and possibly other hormones are released when bacteria ferment indigestible fibres. This stimulates mucosal proliferation and transport in the small intestine. (Massimino et al, 1998)

The mammalian digestive tract can contain several hundred species of microorganisms. They vary depending on a whole range of factors. The faecal flora is different from the one in the body. In the gastro-intestinal system, the microorganism species in the lumen are different from those associated with the intestinal wall. Different segments of the intestine harbour different species. Aside from these differences within the individual animal, microbial populations vary between individuals. This is caused by differences in diet, climatic conditions and even genetics: faecal microbial profiles are more similar in monozygotic twins than in unrelated individuals. (Hooper et al, 2002; Kelly et al, 1994) It is important to emphasize that an animal's diet has a major impact on gut microbiota and intestinal bacterial fermentation (Backus et al, 2002; Carey et al, 2013). The addition of fibre to a diet changes digestibility and faecal metabolites (Kerr et al, 2013). Several studies show positive effects on the health of animals by influencing the fermentation process. Verbrugghe et al, 2010, for example, demonstrates a greater retention of N when fermentable substances are added to the food of domestic cats. This results in the conserving of amino acids so they can be used in other processes such as immunity and tissue preservation.
This offers opportunities to improve the health of cheetahs in captivity by modifying their diet (Kerr et al, 2013).

The intestinal microbiota in cheetahs in captivity seems to be fairly stable. A 3-year study showed about 24% change between consecutive samples in healthy cheetahs. The microbiota is mainly dominated by members of *Clostridium clusters I, XI and XIVa and Lactobacillaceae.* (Becker et al, 2015)

2.3 MICROBIAL FERMENTATION

Fermentation is a process by which microorganisms in the gastro-intestinal tract obtain energy through breaking down dietary and endogenous carbohydrates and nitrogen-containing compounds such as mucus, enzymes or urea without requiring oxygen. Bacterial fermentation produces short-chain fatty acids, ammonia and bacterial protein. The primarily SCFA are acetate, butyrate and propionate. Glycolysis in bacterial cells converts monosaccharides to pyruvate originating the production of ATP (adenosine triphosphate). Pyruvate can be converted in other SCFA resulting in additional ATP production. These SCFA are absorbed through the intestinal wall by passive diffusion. (Hooper et al, 2002) The presence of SCFA creates a more acidic environment in the intestine, which decreases the number of pathogens (Valenzuela et al, 2013).

In sheep, the colonic epithelium uses most of the butyrate for energy production. It also induces epithelial proliferation and differentiation (Pennington, 1951). Acetate enters the bloodstream and is utilized primarily by skeletal and cardiac muscle. Propionate is largely converted to glucose in the liver. SCFA in general influence blood flow and absorptive functions of the intestines. (Bergman, 1990)
Some of the produced ammonia is incorporated in bacterial protein and other ammonia is or absorbed or excreted with the faeces. Bacterial protein is not absorbed and all is lost in the faeces. (Stevens et al, 2004)

Aside from these beneficial metabolites, fermentation also produces a wide number of toxic metabolites. The most common are ammonia, amines, nitrosamines, phenols, cresols, indole etc. (Samanta et al, 2013)

Presence of water in the digesta has an influence on the degree of fermentation. In vitro experiments show that fermentation is accelerated in a watery environment. The intestinal content in cheetahs is rather dry compared to other species, which can be a limiting factor for fermentation. (Kienzle, 1994) Nevertheless fermentation occurs in the gastrointestinal tract in cats and more specific also in cheetahs (Depauw et al, 2011; Sunvold et al, 1995).

A consequence of the presence of carbohydrates in the diet is a decrease of protein digestibility. This is obtained by increased passage rate, endogenous nitrogen excretion, microbial growth and N-fixation. (Kienzle, 1994; Morris et al, 1976)

In cheetahs, animal-derived components can be used by microorganisms for the production of SCFA. Different substrates result in differences in fermentation rate and in the proportions of SCFA produced. (Williams et al, 2001) Cartilage ferments quickly and collagen renders a high acetate to proprionate ratio. The fermentation of protein also produces putrefactive compounds. The diet of felines has a high concentration of protein but the prevalence of diseases associated with these putrefactive compounds is low in free-ranging cheetahs. The discovery of the presence of a microorganism that uses indoles and phenols for growth in the intestines in domestic cats suggests that felines are adapted to the high ratio of protein fermentation. (Depauw et al, 2012) The fermentation of meat generates more putrefactive compounds (Depauw, 2012).
Resent research has shown a decrease in serum indoxyl sulphate in cheetahs fed whole rabbits compared to cheetahs fed supplemented beef. This implies that beneficial fermentation has a positive effect on the animal's health (Depauw et al, 2011).

2.4 ADAPTATIONS TO THEIR CARNIVOROUS DIET

The cheetah is classified in the family of the Felidae, in the Order of the Carnivora (Hunter et al, 2003). As a feline, cheetahs are strict carnivores. Cats cannot adjust the activities of aminotransferases or urea cycle enzymes probably because of the high protein content of their diet (Rogers et al, 1977). Cats have essential nutrients that are not essential in any other mammalian family. It is plausible that, because cats consume high levels of protein, some enzymes have been deleted or altered. (Morris, 2002)

Two amino acids are essential in cats. Taurine is one of the most abundant free amino acids in mammalian tissue (Markwell et al, 1994). The enzymes responsible for the synthesis of taurine from cysteine or cysteinesulphinic acid, cysteine dioxygenase and cysteinesulphinic acid decarboxylase are present but the activities of the enzymes are low (Knopf et al, 1978). Arginine is synthesized from citrulline by the sequential action of enzymes. As in taurine, the activity of enzymes, pyrroline-5-carboxylate synthase and ornithine aminotransferase is low, which results in low levels of citrulline. (Morris, 2002; Morris et al, 1978)

Aside from these amino acids, three vitamins are essential in the diet of cats. Vitamin A is found only in animal tissue while plants contain carotene, its precursor. In cats, the enzyme for cleavage of the carotene molecule has been deleted, making them unable to convert carotene in retinol. (Morris, 2002) A deficiency in vitamin A can result in a range of symptoms but in cats especially it can lead to reproductive disorders (McDonald et al, 2011). This is important in cheetahs because they are difficult to breed in captivity (Marker et al, 1989).

Vitamin B3 is synthesized from tryptophan and cats possess all the necessary enzymes. They also have a high activity of picolinic carboxylase. This enzyme metabolizes tryptophan so that it cannot be

used for Vitamin B3 synthesis. (Morris, 2002) Cats are unable to produce vitamin D through dermal photosynthesis because of a low concentration in 7-dehydrocholesterol (How et al, 1994; Morris, 1998).

Although the most prominent dietary components are protein, cats are able to digest carbohydrates such as glucose, sucrose, lactose, dextrin and starch (Morris et al, 1976). Still some adaptations to the low levels of carbohydrates are present in cats. They lack salivary amylase and have low activities of intestinal and pancreatic amylase. Furthermore, there is a reduced activity of intestinal dissacharidases that break down carbohydrates in the intestines. (Zoran, 2002) Finally, they have a low activity of glucokinase and glycogen synthetase in the liver and the glucokinase is not adaptive (Kienzle, 1994).

These differences in enzymes from other mammals normally do not lead to deficiencies in healthy cats on a natural diet. All essential nutritional compounds are present in animal tissue in sufficient quantities. Therefore, it is believed that these enzyme changes are evolutionary adaptations to the feline diet.

DISCUSSION

This literature shows that the situation in captivity of these felines is partly responsible for a portion of their health problems. This we can conclude because the prevalence of these disorders is much higher in animals in captivity than in wild populations. Furthermore, these are mainly non-infectious diseases. The limited heterogeneity at the level of the HCM loci is therefore not responsible for the high prevalence of these disorders. A final factor to consider in this assumption is that these are disorders that can be explained by the situation in captivity, in particular a suboptimal diet and a stressful situation in which the animals live continuously.

To reduce these disorders in captivity the management of these animals should be adjusted. Stress must be minimized and the diet must be optimized.
The limit of stress can occur in different ways, one of which is modification of their diet. This can be accomplished by not only giving raw meat or a commercial diet but through the use of structure such as bones and hides, e.g. by feeding carcasses. In that way, the animals spend more time eating and there is less time for boredom.
Furthermore, it appears that feeding of carcasses can have a positive influence on the occurrence of the previously mentioned disorders. The non-digestible fibre in the diet could have a protective factor both for the animal to chew longer as regards to oral health and on the level of the digestive system and even once absorbed through the intestinal wall.

Further research to determine to what extent an adaptation of the diet, probably from raw meat or commercial diet to carcasses, can improve the health of these animals in captivity is important. This data can then be passed on to the organisations that house cheetahs in captivity. They can then optimize diet and hopefully reduce the prevalence of these diseases. This can improve the health of the animals in captivity and will possibly induce better breeding results, which will benefit this endangered species.

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