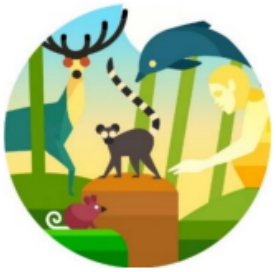
UNIVERSITÀ DEGLI STUDI DI PADOVA

Dipartimento di Biomedicina Comparata ed Alimentazione

Department of Comparative Biomedicine and Food Science

Corso di laurea/First Cycle Degree (B.Sc.)
in Animal Care



WELFARE AND MANAGEMENT OF WILD CATS IN CAPTIVITY: EXPLORING NUTRITION, LEGISLATION AND FEEDING BEHAVIOR

Relatore/Supervisor

Prof. Giorgio Marchesini

Laureanda/Submitted by

Elisa Bizzotto

Matricola n./Student n.

2067301

ANNO ACCADEMICO/ACADEMIC YEAR 2024/2025

INDEX

ABSTRACT: This thesis focuses on the importance of proper management and welfare practices for the conservation of wild cat species in modern zoos and captivity settings. It provides an overview on the role these animals play in various ecosystems and highlights the main challenges faced by keepers and caretakers when managing their welfare. It will more specifically focus on the main nutrition strategies and sources, exploring the potential benefits and drawbacks of providing these animals with whole prey diets and periods of fasting, while taking into consideration species-specific behaviors, needs and ethical concerns associated with this approach.

1. INTRODUCTION - WILD CATS

Wild felids, a diverse group of highly adaptable species, play a fundamental role in the ecosystems they inhabit. In particular, big cats *(Panthera spp.)* such as tigers, lions, jaguars, leopards and snow leopards, are apex predators that directly drive the structure and function of biological communities in various habitats around the world. They maintain biological diversity and ecological richness by acting as sources of mortality for prey populations and significantly impacting the behavior of other species (Krafte Holland et al., 2018).

As keystone organisms, their presence is crucial for maintaining ecosystem balance and health. However, these animals and their conservation has recently become a global priority due to the vulnerable status they occupy in the IUCN Red list. Human-wildlife conflict, defined as “when the needs and behavior of wildlife impact negatively on the goals of humans, or when the goals of humans negatively impact the needs of wildlife”, has become an increasing significant threat together with habitat loss and competition for limited resources, due to the fact that these animals need abundant prey population and large territories to survive while human development and expansion often limits resource availability (Krafte Holland et al., 2018).

Larger species are heavily persecuted because of the danger they pose to humans and livestock, while small cat species are targeted and harvested for fur trade (Lamberski, 2015).

Tension also arises when conservation and human development goals do not align, creating disputes over protected area boundaries, legal responses to incidents, compensation plans, and, sometimes, even loss

of livestock or injury and death to humans and other wild animals (Krafte Holland et al., 2018).
In situ conservation, while essential, is not always effective or achievable in the short term. As a result, much of the effort is focused on ex situ projects and strategies, such as those implemented in zoos, aquaria and botanical gardens together with science, research, invasive species control and the rational and sustainable use of resources through ecotourism (Escobar-Ibarra et al., 2021).
The role of zoos has evolved over the years. Today, these structures have the responsibility of linking both ex-situ and in-situ conservation strategies through various tools and activities, while adhering to animal welfare standards and policies ensuring that it is guaranteed in their facilities. Zoos can complement traditional education with focused conservation messages, allying with universities and institutes, raising funds, taking into account environmental policies and covering the causes of threats, making it easier for people to understand what they can do to help. Species threatened by habitat loss will not be safeguarded unless suitable ecosystems are properly protected, and those at risk of poaching will not be safe until people's attitudes and behaviors change (Escobar-Ibarra et al., 2021).
Ensuring animals are housed in appropriate enclosures and appropriate social groups is critical to their welfare and to improve the public's perception of them, and it's up to professionals, animal care specialists, wildlife advocates and scientists to fulfill this purpose, as animal welfare is an essential tool of the WAZA conservation strategy (Escobar-Ibarra et al., 2021); all zoos must uphold the highest standards to establish and sustain viable populations of healthy animals for conservation purposes and ensure credible conservation messages to all visitors (WAZA, 2005).

2. LEGISLATION AND ETHICAL CONCERNS

2.1 Overview on the main welfare guidelines

Animal welfare refers to a state that is distinct for every individual; it is how the animal experiences its own world and life through its associations with pleasant experiences specific for that species, such as vitality, affection, safety and excitement, or unpleasant experiences such as pain, hunger, fear, boredom, loneliness and frustration (Our approach

to animal welfare - WAZA, 2020). Promoting animal care and protection requires a varied approach in order to minimize the occurrence of negative states and actively promote positive ones. A key aspect of maintaining high standards of welfare is the need for ongoing assessment of an animal's condition (Mellor et al., 2020. WAZA Animal Welfare Strategy).

Negative experiences can generally be classified into two categories: survival-critical behaviors, such as thirst, hunger and pain, which can be easily neutralized through proper husbandry and veterinary care but can never be completely eradicated due to their biological nature, while the second category involves situation-related negative experiences, which include those reflecting the animals' adverse responses to their environment. These can often be replaced or avoided by providing opportunities to engage in rewarding behaviors, such as through environmental enrichments, interactive activities and experiences that stimulate satiety, engagement, goal achievement, interest and curiosity (Mellor et al., 2020. WAZA Animal Welfare Strategy).

The two primary associations for zoo animal welfare, WAZA and EAZA, operate at European and international level, and they recognise the Five Domains Model (Mellor et al., 2020) as the main welfare framework. This model highlights several crucial factors that contribute to animal wellbeing. First, nutrition plays a fundamental role, ensuring the appropriate consumption of nourishing foods and the meeting of daily energy needs, balancing essential and non essential components and guaranteeing that animals receive a proper diet. This diet should be based on scientific evidence and best practice knowledge following expert recommendations. Zoos and sanctuaries should make sure that food has a sustainable origin and that sourcing follows EAZA guidelines when applicable. Furthermore, the quality of feed and water must be inspected before each meal, especially for carnivorous species, where the health of the prey directly impacts their own. Additionally, individual factors such as age, size, growth and reproduction status must be considered and the diet tailored accordingly. Feeding schedules should align with natural patterns, encouraging animals to maintain natural postures and manipulate food in a way that resembles the one of their wild counterparts. When feeding live animals, zoos must follow local

legislations and ensure minimal stress for the prey (EAZA standards for Welfare and Management of Animals in Zoos and Aquariums, 2024).
Following nutrition, the environment in which the animals live is also crucial to their welfare. Facilities must provide high standard enclosures that offer comfort and safety while at the same time reflecting the complexity of the natural habitat they strive to mimic. Minimum recommended enclosure size for felines in zoos is based on the animals' weight, while floor space depends on the number of individuals; small cats range from 3 kg to 20 kg (Mellen, 1997), large cats can reach more than 300 kg (Shoemaker et al., 1997). Each species should have an environment adjusted to their requirements in terms of temperature, humidity, light and ventilation. In these spaces, animals ought to be able to express natural behavior, and the needs of the species, individual and group must be considered (EAZA standards for welfare, accomodation and management of animals in zoos and aquariums, 2024).
Maintaining physical health is another key aspect. This includes performing routine observations as well as having a suitable programme of preventive and curative veterinary care to ensure robustness and vitality. The behavior is also assessed, it's important to encourage activities that involve choice, variety and challenges to promote species-specific traits and reduce stereotypies while regularly measuring and evaluating their effectiveness. Finally, the mental and affective states must be addressed, not only to support natural instincts but also to ensure that physical and psychological needs are being met (EAZA standards for welfare, accomodation and management of animals in zoos and aquariums, 2024).
Understanding public perception on animal welfare is another significant point in order to raise awareness and promote attitude changes. Research indicates that people who do not visit zoos tend to have a negative perception of zoo animals and their living conditions, whereas regular visitors appear to have a more positive view of welfare, naturalistic exhibits and environmental enrichment. Public perception is shaped by a myriad of biological and sociocultural experiences and values. Understanding how society views animal use and captivity, and which factors influence this view, can help stakeholders evaluate what is believed to be acceptable (C. De la Fuente et al., 2017).

2.2 The importance of nutritional management

The nutritional condition of animals kept in captivity plays a critical role in biodiversity conservation, particularly with regards to longevity and reproduction. While older zoos relied on diets tailored to domestic animals together with observations of the feeding habits of free-ranging wild species, modern feeding ecology is grounded in a deep understanding of animal physiology and behavioral needs (Costa, 2014) (Buchini and Gobetti, 2021). The primary objective of nutritional management for wild animals in captivity is to identify their natural dietary habits and replicate an environment and food routine to maintain those standards, while also taking into account food acquisition, storage, preparation and presentation. It must consider the physiological and psychological needs of the species, making sure the adequate amount and type of nutrients is supplied (Diefereld, 1996).

Animal diets are in constant development based on physiological statuses such as gestation, lactation and growth, as well as body condition issues like obesity or anorexia. Clinical/health concerns such as diabetes or food allergies may also require dietary adjustments (Edwards, 2014). Gross and marginal deficiencies or excesses may lead to reduced fertility, suppression of the immune system and even death of captive wild animals. A balanced diet provides the individual with adequate clean water and all of the required nutrients, together with sufficient energy for normal physiological function, without causing any surplus or insufficiencies (Wildon and Kleyn, 2014). Tailoring such specific diets involves several steps, the first consists in determining which diet items the animal will readily accept in order to ensure its survival, followed by the supplementation of these items with essential nutrients like minerals and vitamins. The next step is replacing convenient dietary provisions with something that resembles, in chemical composition as well as physical structure, the animal's natural diet, expanding the biochemical understanding of nutrition and linking its interactions with larger anatomical structures such as dentition and gastrointestinal anatomy, providing them in species-appropriate ways to achieve behavioral management goals (Frens and Clauss, 2024. Journal of Zoo and Aquarium Research).

3. WELFARE AND DIET

3.1 Wild cats' natural diet

Forty-one surviving felid species exist today, grouped within two families: *Pantherinae* and *Felinae*. These species possess a multitude of physical characteristics, each combining into a singular morphology that is considered similar among all cats (Greene, 2022). Many of these shared physical traits can be attributed to an overall form adapted and evolved for hunting to meet the specialized hypercarnivorous diet which all cats thrive upon. This specificity has resulted in a number of physiological, biochemical and anatomical adaptations. Members of this species require a higher percentage of protein in their diet and possess a body structure that reflects an ability to hunt, capture and kill live prey (Greene, 2022). Several key diet-related physiological traits include differences in digestive enzymes, shortened digestive tracts, changes in amino acid dietary requirements and alterations to taste bud sensitivities (including a heightened response to amino acids and a loss of response to many mono- and di-saccharides). In addition to these, the morphology of cats is highly adapted to predation and includes flexible bodies, fast reflexes and strong muscular limbs, together with a strong night vision and hearing, crucial for hunting (Kim et al., 2016). Research has shown that while hypercarnivory has no effect on taxonomic diversity, it has a strong effect on morphological diversity related to jaws and dentition (Holliday and Steppan, 2004).

The diet of wild felids varies depending on their sizes. Large cats, such as lions and tigers, typically prey on very large mammals, with only two to three species making up the majority of their diet. Medium-sized felids such as pumas, snow leopards and leopards target smaller prey but from a wider variety of different species. Small felids feed on mammals, birds, reptiles, amphibians and insects. All of them generally hunt and kill, some engage in scavenging behavior (Lamberski, 2014).

While bigger carnivores, like the European lynx, can obtain a higher net energy intake by hunting on medium-sized animals such as roe deers, the difficulty of capturing this prey results in a greater energy expenditure compared to that of small-prey specialists (Carbone et al., 2007). Wild carnivores typically shift from hunting small to medium and large prey at a body mass of about 20 kg (Carbone et al., 1999). A bigger prey size

generally implies a bigger meal, unless it has to be shared among many individuals, which reduces the individual meal size to levels similar to that of solitary predators that target smaller prey (Hornocker, 1967) (Owen-Smith and Mills, 2008). Additionally, increasing meal size also leads to decreasing feeding frequency and hunting behavior, driven by hunger (Hall and Bradshaw, 1998) (De Cuyper et al., 2016).

3.2 Captivity

Proper feeding management of wild animals in captivity combines both husbandry expertise and applied nutritional science (Dierenfeld, 1997). To meet the nutritional and behavioral needs of all species, it is recommended to implement a formal nutrition program. Diets should be designed in accordance with the guidelines of nutritionists such as the European Association of Zoos and Aquaria (EAZA) Nutrition group or the Association of Zoos and Aquarium (AZA) Nutrition Advisory Group (NAG). These organizations suggest a strategy that ensures diets are nutritionally balanced, reasonably stimulate natural feeding behaviors, are consistently consumed by the animal, and meet specific criteria, while also being practical and cost-effective (Lamberski, 2014).

As discussed in earlier chapters, the quantities of food provided should be adjusted based on the animal's body condition, life stage and environmental factors. Exotic feline diets are usually higher in fat, protein and vitamin A. A diet suitable for most cat species contains 40%-50% protein, 30%-35% fat, 3%-4% crude fiber, 1.2%-1.5% calcium, 1%-1.2% phosphorus and 20,000-40,000 IU of vitamin A/kg diet (dry matter basis). Exotic cats are unable to convert carotene to vitamin A, tryptophan to niacin, and linoleic acid to arachidonic acid. They also cannot synthesize adequate taurine and are susceptible to ammonia toxicity if fed an arginine-deficient diet. Therefore, these nutrients should be considered dietary essentials for all felids (Nijboer, 2024).

Most captive facilities provide felids with a diet of ground meat supplemented with vitamins (Hartstone-Rose at al., 2014). Frozen and canned cat foods usually are more palatable than dry ones to exotic cats. Many zoos prefer to use frozen diets because generally they are less expensive and large quantities are easier to feed. The soft consistency of commercial diets can result in excess calculus deposits and periodontal disease if hard or unprocessed items are not provided,

which implies that cats should receive bones with some meat intact twice weekly (Nijboer, 2024).
Items such as rodents, poultry or rabbits, can be offered regularly or periodically instead of, or in addition to, commercial diets, to enhance dietary diversity (Hickman et al., 1990; Mellen et al., 1998).
The aim is not only to support animal welfare but also to maintain oral health due to the abrasion that bones cause on the teeth, preventing tartar build up. However, it's important to avoid excessive supply of this type of food, as it can lead to abnormal tooth wear, loss of enamel or general dental damage. Fresh water should also always be available (Buchini and Gobetti, 2021).
Additionally, as mentioned earlier, animal feed should be routinely analyzed for nutritional content, bacterial contamination and the presence of foreign materials. While most felids can tolerate large concentrations of microorganisms in raw meat, each institution should establish guidelines for acceptable bacterial amounts in commercial products (Lamberski, 2014).
The types of food offered, as well as the differences in nutritional requirements throughout the year, should also be considered. Wild cats typically share the same nutritional needs as domestic cats, although there is evidence that some species differ with respect to selected nutrients, but from a comparative perspective, these animals are relatively easy to maintain nutritionally (Mellen, J.D, 1997). To determine the most appropriate and effective nutritional approach, it is essential to conduct a thorough nutritional assessment. This allows for the identification of malnourished animals who might need immediate intervention, as well as those who could benefit from nutritional therapy in the prevention of malnutrition and obesity. Each individual animal should be weighed and its energy maintenance needs estimated in kilocalories of metabolizable energy per day (Fabretti et al., 2020).

3.3 The role of nutrition on physical and mental health

Nutrition is essential for maintaining normal physical and physiological functions in animals, as well as ensuring their overall health. Key nutrients such as carbohydrates, protein, minerals and vitamins each play distinct roles in supporting the body's normal functioning. A lack of adequate or balanced nutrients and/or unbalanced feeds can lead to

insufficient nutrition, starvation, emaciation, immune deficiencies and increased susceptibility to disease along with other disorders. On the other hand, overfeeding certain nutrients may also lead to toxicity or sickness (Shukla et al., 2014). Even though zoos, aquariums and sanctuaries aim to provide diets that closely replicate the nourishment felids would acquire in the wild, nutrition alone is not enough to fully satisfy a wild animal's physiological requirements. The consistency, texture and mechanical properties also matter, as they affect both dental health and cranial morphology. A diet that more closely mimics that which would be found in nature could prevent negative changes caused by the physiological under-stimulation pervasive in captive settings, such as dental problems due to the lack of abrasive action (Hartstone-Rose et al., 2014).

Though captivity does not provide animals the opportunity to forage or hunt as their wild counterparts would, the instinct to do so remains. Some zoos have addressed this with feeder mechanisms that stimulate movement, such as lure courses for cheetahs and bungee cord feeders for lions and tigers, together with pole feeding (Hartstone-Rose et al., 2014) (Fig. 1).

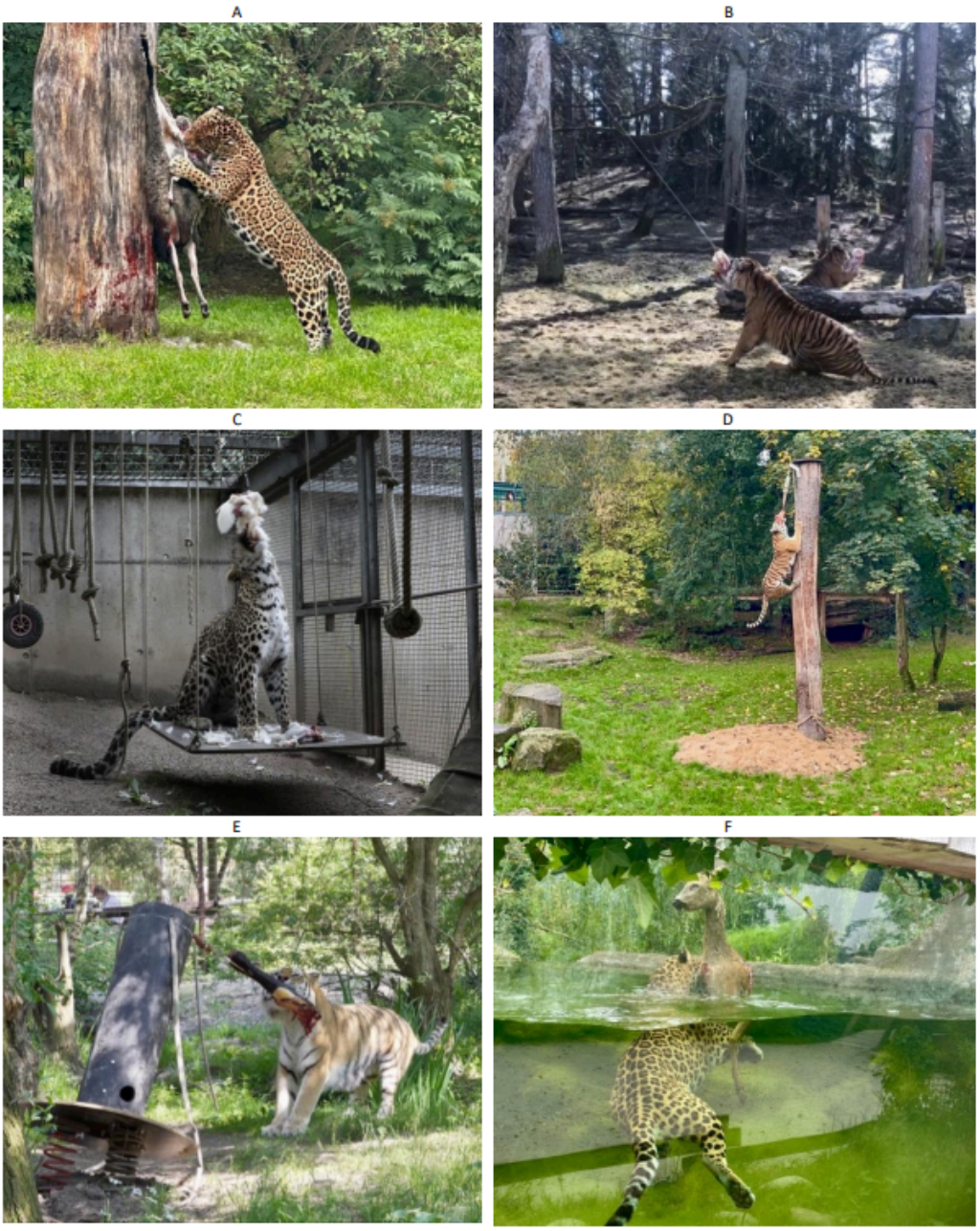


Fig. 1. Examples of different feeding methods for large carnivores: (A) carcass tied to a tree, Parken Zoo, Sweden; (B) counter-pulling system for two animals, Parken Zoo, Sweden; (C) swinging platform – Cologne Zoo, Germany; (D) pole feeding, Cologne Zoo, Germany; (E) self-built feeding object, Odense Zoo, Denmark; (F) food presented over water, Randers Regenskoven, Denmark. 1C copyright by Dr. A. Sliwa, Cologne Zoo; all other photos: Cellina Kleinlugtenbelt/Anita Burkevica (Kleinlugtenbelt, 2023)

Not having stimulation has been shown to lead to stereotypical and abnormal behaviors such as over-grooming, lethargy and pacing. Several studies have found that the implementation of enrichment like bones, spices or frozen fish, caused a significant decrease in

stereotypies encouraging natural habits that may prevent physiological and anatomical changes in captive animals. Even though the morphological effects of an unnatural diet consistency have not been fully explored, dietary supplementation is an important component of psychological enrichment (Hartstone-Rose et al., 2014).

Specific items have proved to elicit appetitive behaviors that might be seen in the wild, such as rubbing and rolling with the addition of cinnamon and cumin on the ground and logs of the enclosure, together with object manipulation and searching when provided with bones and fish (Skibiel et al., 2007). Observations seem to suggest that changes in activity level and stereotypic behaviors following enrichment may differ among species. During a research conducted by Amy L. Skibiel, all the species exhibited an increase in active behavior when provisioned with bones and frozen fish compared to baseline, and five of the six species when provisioned with spices (Fig. 2) (Skibiel et al., 2007).

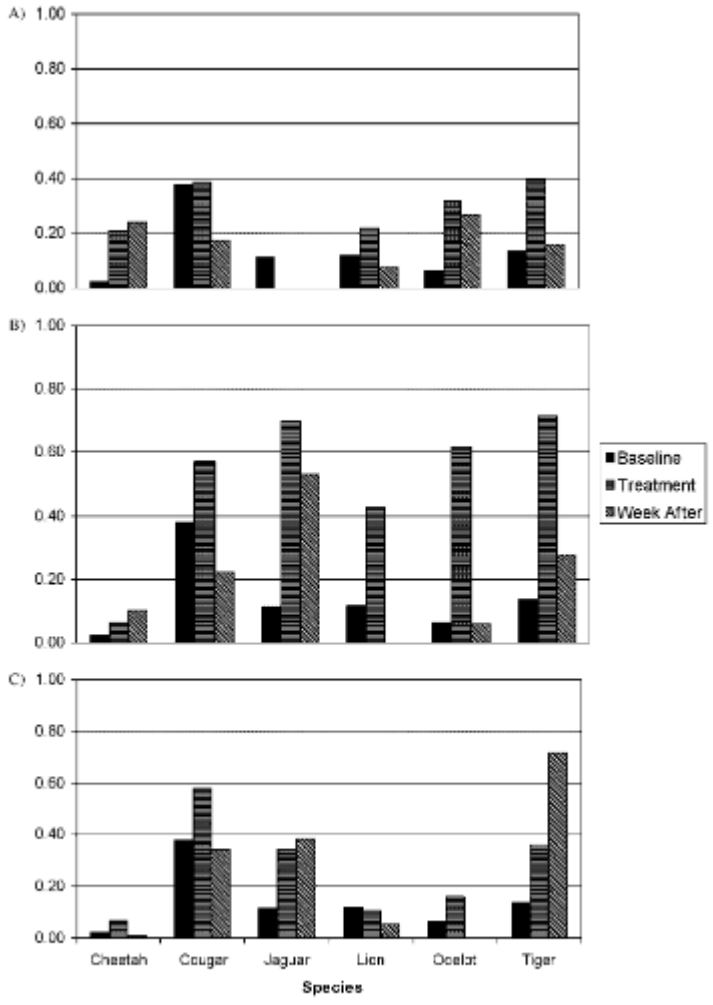


Fig. 2. The proportion of behaviors classified as active averaged among individuals for each species of felid for each treatment: (A) bones, (B) frozen fish, and (C) spices. The jaguar did not participate in the bones treatment (Skibiel et al., 2007. Zoo Biology)

A decline in stereotypic behaviors was seen for all species that exhibited stereotypies during baseline observation (Fig. 3).

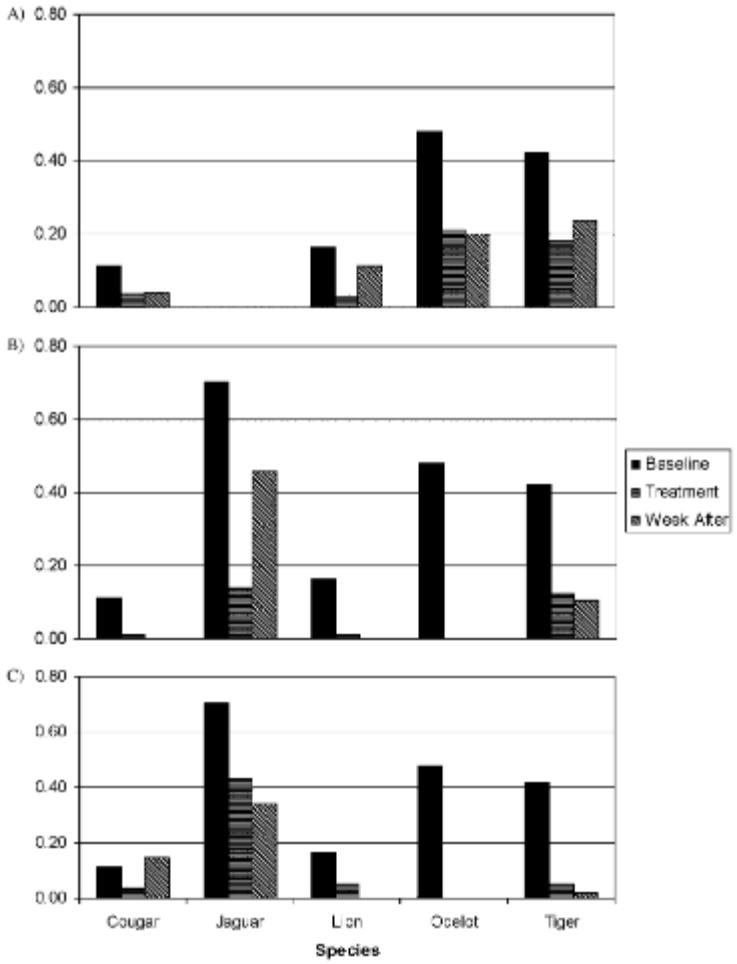


Fig. 3. The proportion of active behavior that were considered stereotypic averaged among animals for each species of felid for each treatment: (A) bones, (B) frozen fish, and (C) spices. The jaguar did not participate in the bones treatment. Cheetahs did not exhibit any stereotypic pacing during the course of the study. With the addition of spices and frozen treats, no stereotypical pacing was recorded for ocelots (Skibiel et al., 2007. Zoo Biology)

Moreover, feeding enrichment is designed to provide animals with an opportunity to use natural foraging strategies to obtain food in captivity (Bashaw et al., 2003).

4. WHOLE PREY FEEDING: BENEFITS, CHALLENGES AND ETHICAL CONCERNS

4.1 What is whole prey?

Although nutritionally balanced formulations, largely based on the nutrient requirements of domestic cats, are commercially available for many zoo carnivores, some choose to incorporate whole prey as a part or all of certain captive feeding programs. Whole prey more closely resembles the physical form of the natural diet of these animals and is often assumed to fulfill their nutritional needs, provided that nearly all soft tissues and some bones (or other calcified tissues) are consumed (Dierenfeld et al., 2002).

In the wild, animal tissue provides all nutrients required by felids. Their digestive system is composed of a simple stomach, short digestive tract, and well developed canine and carnassial teeth for tearing and gripping flesh. Compared to omnivores, felids have evolutionarily lacked the need for rapid adaptation to a variety of diet types and are metabolically prepared for the high metabolism of protein and fat, with less emphasis on the utilization of carbohydrates. As a result, these animals have many unique dietary requirements, including high protein, taurine, and tyrosine together with an obligate requirement for arginine (Kerr, 2012).

The size of the prey is commonly related to the consumer's body size, and the species offered often reflect the documented or perceived natural feeding habits together with the animal's individual preferences (Dierenfeld et al., 2002).

Whole prey items, when used, represent the most expensive part of a carnivore's dietary program. Therefore, it is crucial that methods of procurement, receipt, handling and storage preserve their nutritional value and maximize the benefits of their use, as they directly influence the cat's health. Generally, carcasses provide substantial amounts of crude protein, often exceeding the requirements for domestic carnivores. Since there have been no significant reports of amino acid deficiencies, and given the high concentrations of protein in prey, it is likely that amino acid requirements will be met. Furthermore, the crude fat content in most carcasses is also significantly higher than the recommended minimum levels for domestic carnivores. Neonatal prey animals have lower body fat concentrations compared to older ones, and skinned, eviscerated

carcasses have lower fat content than whole bodies of prey animals of the same age. Assuming that the fatty acid requirements of zoo carnivores are similar to those of domestic cats, available studies on the fatty acid composition of whole prey suggests that essential fatty acid supplies are adequate. However, peroxidation due to extended or improper storage can result in declines of essential fatty acid activity and destruction of vitamin E. Mineral concentrations can also vary widely depending on prey type and, to some extent, prey age. Neonates often, but not always, tend to have lower proportions of total ash compared to adults. Vitamin A content increases with age and maturity through accumulation of body stores, particularly in the liver, which serves as the major storage organ for this vitamin. The vitamin E concentrations in most of the analyzed carcasses appear to meet the estimated dietary requirements of domestic dogs and cats, provided that their diet includes moderate levels of polyunsaturated fatty acids (Dierenfeld et al., 2002).

4.2 Benefits of whole prey diets

There are relatively few researches exploring the benefits of whole prey diets for captive felines. A notable study, conducted at Parken Zoo, in Sweden, and published in the Journal of Zoo and Aquarium Research in 2023, investigated the behavioral effects of feeding lean meat versus feeding whole rabbits to zoo-housed jaguars.

Over a ten day period, three jaguars were fed either lean beef or whole rabbit/sheep carcasses. Researchers observed and recorded the jaguars' behavior during and after feeding, focusing on the time spent engaging in natural foraging activities such as tearing, manipulating and consuming food (Enemark et al., 2023).

The results revealed significant differences in the feeding behavior of the animals depending on the type of food provided. When given whole carcasses, they spent considerably more time engaged with the prey, particularly in the first hour after feed presentation. Irrespective of the feed type, feeding behavior only occurred during the first hour (Fig. 4)

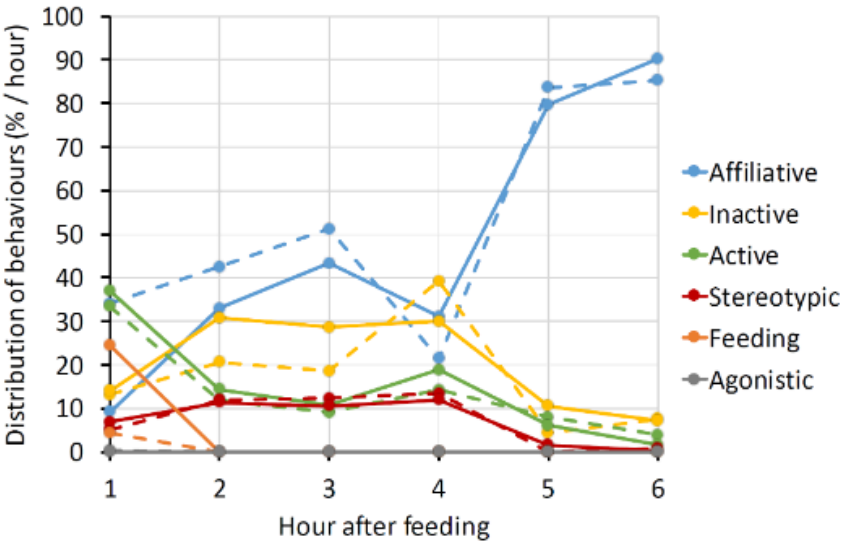


Fig. 4. Distribution of different behaviours during six hours post feeding for jaguars *Panthera onca* fed whole prey (solid lines) or lean meat (broken lines) (Enemark et al., 2023. Journal of Zoo and Aquarium Research)

Figure 4 shows that feeding aroused the jaguars, and that depending on the effort required, they were either less inactive afterwards and showed more social behavior (when fed lean meat) or had higher levels of inactivity (when fed whole prey). Specifically, in this particular group of jaguars, agonistic behaviours were extremely rare and therefore increased general activity led to a more distinct increase in affiliative rather than agonistic behavior. This should not be interpreted as a social behavior-stimulating effect of lean meat, but as a general state of arousal that in this particular group led to more positive interactions (Enemark et al., 2023).

The time spent feeding increased by over 300% when the jaguars were provided whole rabbits compared to lean beef, indicating that carcasses encourage more natural, species-specific activities. Despite these results, however, the overall impact on the jaguars' daily patterns was minimal, in terms of the overall proportion of a 24-hour budget this represents a change of less than 1%, suggesting that while whole prey did, in fact, increase feeding behavior, it did not significantly affect their overall behavioral patterns. Greater increases in feeding time and a larger effect on the other behaviours could potentially be achieved by providing larger carcasses and by making the feed harder for the jaguars to acquire (Enemark et al., 2023).

Ultimately, the study highlights that carcasses can serve as an effective form of environmental enrichment for captive jaguars, also promoting hunting-related activities and contributing to an overall mental and physical well-being. However, the limited behavioral impact suggests that these practices should be complemented by other forms of enrichment to more effectively enhance the animals' welfare (Enemark et al., 2023).

In a separate study by M. Elsbeth McPhee at Toledo Zoo, Potawatomi Zoo and Binder Park Zoo, the impact of offering intact calf carcasses as environmental enrichment for captive wild cats was explored. Over a 14-week period, nine felids were provided with intact, eviscerated calf carcasses. Behavioral observations both on and off exhibit revealed that offering this type of diet led to reduced off-exhibit stereotypic behaviors as the animals engaged in more natural activities such as tearing, chewing and using their teeth and claws. However, the carcasses did not consistently reduce the stereotypic behaviors observed on-exhibit, not affecting the way these animals behaved in front of zoo visitors, likely due to the challenges posed by conducting the research across multiple institutions and on a small number of cats (McPhee, 2002).

Similar results were reported in a study conducted at Chester Zoo on a 9 year-old female Asiatic lion. This research explored the effects of offering a whole calf carcass on the lion's behavior in three distinct regimes. Pre-carcass regime: 11 days pre-diet change; post-carcass regime: 11 days shortly after the carcass feeding regime had started, and 12 months post carcass regime: 11 days of data collected 12 months following the diet change.

Here, again, the results indicated an increased feeding time and resting behavior at about 12 months post-carcass feeding together with a massive decrease of pacing (Fig. 5 and Fig. 6) (Finch et al., 2020. Journal of Zoo and Aquarium Research).

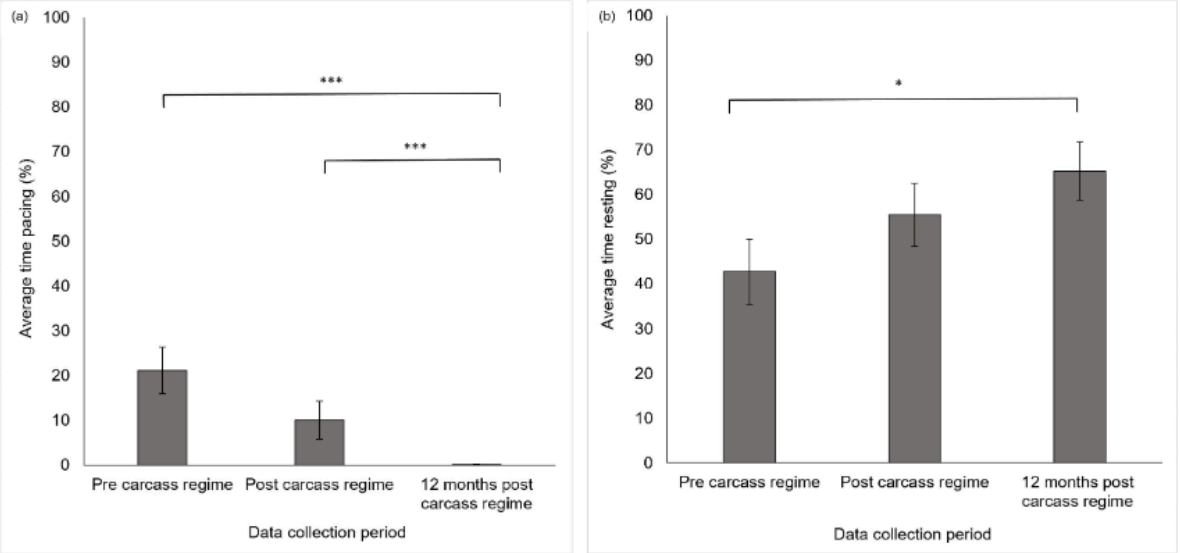


Fig. 5. Average time study individual engaged in pacing behaviour (a) and resting behaviour (b) across the three data collection periods (Finch et al., 2020. Journal of Zoo and Aquarium Research)

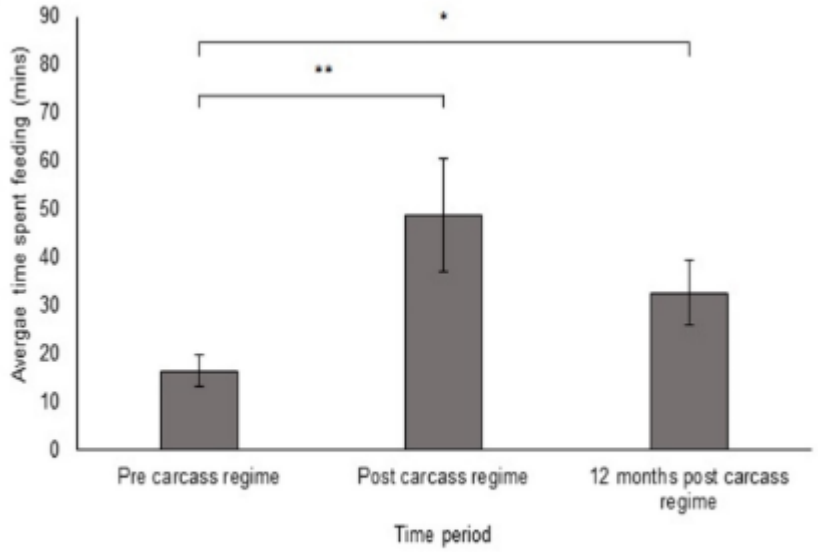


Fig. 6. Average time spent feeding across the three data collection periods (Finch et al., 2020. Journal of Zoo and Aquarium Research)

Changes, though, were not immediate, probably due to the fact that the physiological and psychological adaptations to a gorge and fast routine requires time (Finch et al., 2020. Journal of Zoo and Aquarium Research).

The nutritional benefits of whole prey diets have also been explored. A study by Sarah Depauw investigated the role of animal-derived fiber in maintaining gastrointestinal health in cheetahs, which are obligate

carnivores. In a cross-over study, fourteen cheetahs were randomly assigned to two diet groups and fed either whole rabbit, including skin, fur and viscera, or chunked beef for three consecutive weeks. After each adaptation period, individual fresh faecal samples were collected and calprotectin was analyzed to assess gut health and the possible presence of inflammation. The results were evaluated using in vitro fermentation to observe how the different dietary components affected the activity of gut microbiota and microbial fermentation. Cheetahs have a strict diet consisting mostly of meat, but their digestive system also requires specific dietary fibers that are typically found in undigested parts of the prey such as bones, skin, cartilage and hair. Additionally, a dietary survey was conducted across 86 zoos and facilities housing 184 captive cheetahs with the aim of collecting general data about the animals' diets, health parameters and gastrointestinal conditions, specifically assessing fecal consistency, vomiting and diarrhea to understand the possible link with the diet. The animal fibers provided through the ingestion of whole prey elements appeared to support healthy microbial fermentation in the cheetahs' hindgut, together with the stimulation of the fermentation process, crucial for healthy digestion and nutrient absorption, with hair acting as an insoluble fibre. The poorly digestible animal tissue included in the whole rabbit may act as a bulking agent, filling the colon and providing a physical barrier between bacteria and substrate, which might be an effective mechanism to prevent or reduce spikes in protein fermentation (Depauw et al., 2013). Through the survey and health assessment data, the study found that the use of muscle meat, with or without carcass components, was associated with an improved gastrointestinal health status, in contrast to the use of commercially prepared diets. Vomiting and diarrhoea were also less likely to occur in animals that were fed carcass components (ribs and long-bones), while muscle meat-fed cheetahs were at reduced risk of gastritis and other gastrointestinal issues, as well as having improved faecal consistency. Interestingly, specific prey species were identified as having a significant impact on the risk of gastrointestinal disease during univariate analysis; for example, chicken was found to have a protective effect, but horse and goat meat showed to increase the risk of gastritis and vomiting (Whitehouse-Tedd et al., 2015). Overall, these findings highlight the need to improve the understanding of the effects of whole prey diets on

gastrointestinal function in cheetahs and other exotic felids, highlighting the importance of fermentation processes on the overall health of these animals and introducing a novel area of interest relevant to the welfare of captive feline species (Depauw et al., 2013).

4.3 Drawbacks and challenges of whole prey

While this practice provides several benefits to carnivores by offering a diet that closely mimics what they would find in the wild, nutritionally and mechanically, many zoos in Europe and North America remain hesitant to adopt it. Concerns include the potential safety risks, such as the possibility of predators choking on carcass elements, food spoilage before it is fully consumed or animals fighting over large prey items (Hartstone-Rose et al., 2014). Additionally, sourcing, preparing and storing whole prey also presents challenges, and institutions that choose this feeding method should be aware of potential hazards such as pathogens and parasites. Proper precautions must be taken to minimize risks and ensure that the carcass is safe (Feeding of Vertebrate Animal Carcass and Whole Body Prey Statement. NAG, 2013).

Zoos that receive intact animals have the option of either discarding the hide or using it as a behavioral enrichment product. If whole animals that are received for use require further processing, such as head or hide removal, they should be processed in areas separate from any other food preparation zone to avoid cross contamination. Carcasses and whole prey should be defrosted in a controlled manner, preferably in a refrigerator for a 24 to 48 hour period prior feeding to minimize the tissue damage caused by rapid thawing (Feeding of Vertebrate Animal Carcass and Whole Body Prey Statement. NAG, 2013).

Another important thing to consider is that, even though carcass feeding can encourage natural behaviors, studies have shown mixed results. While it reduces stereotypic behaviors in snow leopards, leopards and lions, it has been shown to increase pacing behavior in tigers (Sutherland et al., 2021), suggesting that its effects can vary depending on the type of carnivore, environmental factors or individual preferences.

Moreover, if the prey is not entirely consumed and begins to spoil, it could pose a threat to the animal's health. On the other side, excluding specific key components, such as organs or gastrointestinal contents, could lead to nutritional gaps or imbalances. Additionally, large or tough

prey items may create choking hazards or cause injury, together with the possibility of initiating competition or fighting and causing stress particularly in multi-animal enclosures (Sutherland et al., 2021). The act of consuming large prey might also not fully replicate the complexities of wild diets, potentially causing behavioral issues. Therefore, all of the above factors should be carefully managed and understood to ensure the health and well-being of the animals.

4.4 Ethical concerns and public perception

The Association of Zoos and Aquariums (AZA) outlines specific guidelines for the ethical acquisition and management of vertebrate feeder animals. According to these guidelines, feeder animals should be sourced responsibly, with an emphasis on ethical considerations. Wild-caught animals must be collected in a manner that does not threaten the sustainability of their populations or disrupt the ecosystems they live in and, whenever possible, zoos are encouraged to prioritize the use of captive-bred animals to reduce the impact on wild populations. All prey sourcing practices must comply with relevant laws and conservation standards to prevent overharvesting or exploitation. Additionally, feeder animals should be housed in environments that meet their species-specific needs, ensuring they are kept in conditions that aim at reducing stress and preventing harm. During transportation, zoos must minimize travel times and follow humane handling practices. Proper care also includes maintaining the animals' health through appropriate nutrition and veterinary attention and, if euthanasia is required, it should be done humanely and in line with veterinary guidelines to guarantee a quick and painless death (Guidelines for the humane and ethical acquisition and management of vertebrate feeder animals (excluding fish). NAG 2017).
Public education is also encouraged to help visitors understand the necessity of whole prey in maintaining the health and vitality of the carnivores they see in captivity, and zoos should be transparent about their feeding practices, addressing the emotional concerns of people and explaining how this method contributes to the animals' well-being and natural behavior. Records of all feeder animals should be maintained, documenting species, breeding practices, health checks and transport

conditions (Guidelines for the humane and ethical acquisition and management of vertebrate feeder animals (excluding fish). NAG 2017).
Institutions such as the Nutrition Advisory Group to the Association of Zoos and Aquariums further recommend that facilities should acquire carcasses only from inspected sources and whole body prey from licensed vendors. The use of “road kill” should be discouraged, as should the acceptance of donated carcasses and prey animals, unless it can be established that they come from a safe source.
A study conducted by Ellen K. Roth, aimed at assessing visitor comfort and attitudes towards carcass feeding at the ABQ BioPark Zoo, found that, while research has explored visitor perceptions of zoo animals and enrichment techniques, there has been limited focus on reactions and comfort levels during carcass feedings. Visitors tend to connect with animals that are active and display natural behaviors, and carcass feeding has been shown to increase activity and encourage natural habits. Based on this, one might predict that visitors would be content and engaged with carcass feeding due to its positive effects on the animals. However, the use of vertebrate mammals as prey rather than inanimate objects like an old tire or a tree branch seems to present an interesting dilemma (Roth, 2017).
Research into zoo visitors’ perceptions of carcass feeding reveals a generally positive response, with many visitors comfortable and engaged with the practice. Studies conducted at Western Plains Zoo and Monatro Zoo found that a significant majority (69.5% and 85% respectively) approved of this practice, and most were not offended by it. Many recognized its educational value, with nearly all respondents appreciating the role it has in showcasing naturalness. Approximately 30% of visitors even considered carcass feeding essential for the well-being of the animals (Roth, 2017).
Roth's study also showed that visitors tend to watch animals in exhibits longer when a carcass is introduced and are generally at ease with observing the feeding. Many expressed that the practice seemed natural to them or that they believed it was a positive thing for the animals even if it made them uncomfortable.
These findings can help guide various zoos in making decisions surrounding this strategy and its relation with the comfort of the visitors (Roth, 2017).

5. FASTING AND FEEDING SCHEDULES

5.1 Natural feeding patterns

The free-ranging counterparts of captive felines neither have a fixed schedule nor eat daily. Many large mammalian terrestrial carnivores do not hunt every day in their natural habitats, because given the right prey, they can gorge-feed more than their daily energy and nutrient requirements. Several studies have reported, for example, that lions eat at an average frequency of once every 2.5 days on plains and once every 3-3.5 days in woodlands. Hunting success rates also vary a lot with seasons and habitats, kill frequency is not necessarily linked to carnivore body size, so there's no consistent decrease in carnivore feeding frequency with species' body mass. Feeding frequency depends on predator body mass range and the size of the prey habitually taken as a species, in a specific habitat or at a specific time of the year. Whenever large carnivores subdue large prey and conditions are favourable to gorge-feed, until the limits of their maximum gut capacity are reached, they can ingest energy in excess of their daily requirements within a short period of time. Thus, if they are not in a metabolic state of accumulating body stores for periods of hibernation, large predatory mammals in natural habitats do not necessarily have to hunt every day, allowing them to be "full and lazy" (Kleinlugtenbelt et al., Journal of Zoo and Aquarium Research, 2023) (Fig. 7).

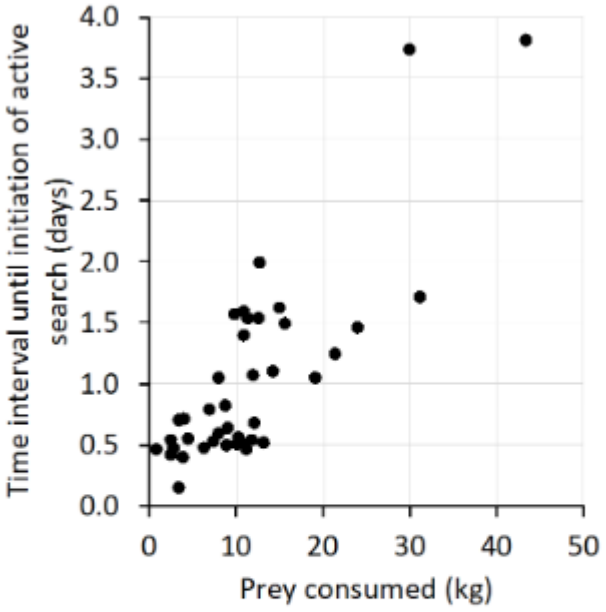


Fig. 7. Relationship between the amount of prey consumed for a lion *Panthera leo* and the time until the next search for prey is initiated. Data extracted from Elliott et al. (1997) and converted from hours into days, and from calories into kg, using the given conversion factors. When consuming less than 10 kg of prey, the next search was initiated within a day. Note that due to different energy expenditure between free-ranging and zoo-managed lions, the amount of prey consumed cannot be considered a recommendation for zoo animals; however, the data serve to illustrate the amount of prey considered to cause gut fill-related satiety with a consecutive "lazy" day (Kleinlugtenbelt et al., 2023. Journal of Zoo and Aquarium Research).

5.2 Fasting in captivity

Fasting days are part of the regular schedule in large carnivore zoo husbandry for many species. Allen et al. (1996) states that "many zoos fast their large cats 1 day per week", suspecting that even in the absence of scientific evidence, occasional fasting is probably beneficial for animals that receive little exercise and are prone to obesity. This approach reveals how a zoo's husbandry can match or deviate from conditions encountered in natural habitats, questioning the biological background of such management decisions. Many large felids are known to often have an alternating pattern of more active hunting, gorge-feeding days and days spent resting and digesting, in contrast to small felids, which are considered to hunt and eat several times per day and for which fasting should probably not be used in captivity (Kleinlugtenbelt, 2023).

In a paper published in the Journal of Zoo and Aquaria Research, Kleinlugtenbelt and other researchers collected husbandry guidelines and results that covered this specific topic for big cats.

Data from 44 zoos in 7 countries were put together during personal visits. Regarding felines, the species observed were tigers *(Panthera tigris)*, lions *(Panthera leo)*, jaguars (*Panthera onca)*, leopards (*Panthera pardus)*, snow leopards *(Panthera uncia)*, cheetahs *(Acinonyx jubatus)* and lynxes (*Lynx lynx)*. The study revealed that hunger periods are commonly recommended in husbandry guidelines for large carnivores, including all large felids. These guidelines, originating from well known organizations such as EAZA and AZA, typically suggest one or two meal-free days per week, and two fasting days are repeatedly stated as a maximum (Kleinlugtenbelt, 2023).

Some challenges faced during this study include whether or not feeding intervals effectively mimic natural foraging and hunting behaviors. These days are generally aimed at obesity management, promoting dental health through bone feeding and provision of enrichment. For felines, fasting is often considered beneficial in terms of managing weight and maintaining natural instincts related to predation and foraging. However, for some of them, like the cheetah and the lion, some guidelines explicitly state that these types of days are not essential, suggesting that this practice is not universally applied to all big cats (Kleinlugtenbelt, 2023) (Table 1).

Species	Fasting day recommendations	Source
Tiger *Panthera tigris*	One or 2 fasting days/week improve appetite and body condition	Dierenfeld et al. 1994
	On fasting days, large bones can be fed for dental health and as enrichment	
	Two fasting days/week during which bones can be fed for dental health/enrichment	
	Fasting days during which large bones and whole prey can be fed to stimulate the gastrointestinal tract and avoid impaction	Baker 2006 AZA Tiger SSP 2016
	Fasting days do not reflect wild gorge-fasting foraging behaviour	
Lion *Panthera leo*	Fasting days are not essential	Hillermann 2009
	Example of two fasting days/week with chicken neck feeding on second fasting day	
	Fasting days of less than 24 hours are common in many zoos	AZA Lion SSP 2012
	Animals should not be fasted more than 2 days/week	
Jaguar *Panthera onca*	Fasting days of less than 24 hours are common in many zoos	EAZA 2022
	Fasting days do not reflect wild gorge-fasting foraging behaviour	SSP 2007b
	Fasting days are useful for body weight management	
	Bones can be fed during fasting days	
	Fasting days of less than 24 hours are common in many zoos	AZA Jaguar SSP 2016
	Animals should not be fasted more than 2 days/week	
Snow leopard *Panthera uncia*	Recommendation of weekly fasting	Alankar 2014
	On fasting days, large bones can be fed for dental health and as enrichment	
	Fasting days are useful for body weight management	
Clouded leopard *Neofelis nebulosa*	Recommendation of 1 or 2 fasting days/week	SSP 2000
	On fasting days, large bones and small whole prey can be fed	
Cheetah *Acinonyx jubatus*	Previous recommendation of 1 fasting day/week, however, no proof of health effects	EAZA 2018
	Fasting days do not reflect wild gorge-fasting foraging behaviour	
	Fasting days without preceding gorge feeding day might be contraindicated	
	One or 2 fasting days/week improve appetite and body condition	SSP 2009
	Large bones can be fed on fasting days for dental health	
	Recommendation of 1 fasting day/week and an increase of meal size on feeding days	
	Fasting days might be contraindicated and cause stress	
	Recommendation of 1 fasting day/week and an increase of meal size on feeding days	Marker and Schumann 1998
	Fasting days are not essential	
	One or 2 fasting days/week improve appetite and body condition	
	Large bones can be fed on fasting days	
Eurasian lynx *Lynx lynx*	Recommendation of 1 or 2 fasting days/week	EAZA 2004

Table 1. Summary of fasting day recommendations from husbandry guidelines (Kleinlugtenbelt et al., 2023. Journal of Zoo and Aquarium Research).

Additionally, whereas some texts imply that fasting days serve to mimic natural foraging behavior, others specifically state that they do not fulfill this function. These periods are framed to simulate the natural cycles of feast and famine, however, the research suggests that this does not

thoroughly replicate the natural feeding patterns of felines, because, in the wild, they typically experience alternating periods of gorging and rest after hunting and consuming large preys, while in captivity the fasting days do not always correspond to this natural cycle, as they are often implemented for reasons other than behavioral enrichment. Only one (cheetah, EAZA 2018) out of 24 husbandry guidelines mentioned specific recommendations for the feeding practices preceding the fasting day, such as the necessity to gorge-feed in order to obtain positive effects on the behavior and avoid an increase in abnormal stereotypies. Interestingly, some protocols, like those for tigers and cheetahs, also recommend increasing the amount of food provided on feeding days in order to compensate for the food intake lost during fasting days. This approach is meant to ensure that the animals receive appropriate nutrition without compromising their health (Kleinlugtenbelt, 2023).

The survey revealed that the majority of zoos used fasting for felids, and of those that applied this method, many took it as an opportunity to perform training that included a food reward, especially with leopards, partially to compensate for an increased propensity to stereotype on these days. However, the survey also indicated that fasting days are not always accompanied by increased physical or cognitive challenges for the animals, which could lead to issues such as increased pacing or unwanted behavior. For felines specifically, the lack of structured physical and cognitive enrichment might contribute to a lack of engagement, making it feel less like a natural rest day and more like a day of inactivity. While some zoos have successfully incorporated these hunger periods as part of their management strategies, the lack of evidence supporting their efficacy for obesity control or the simulation of natural behaviors means that alternative methods should be explored. Moreover, the feeding practice observed in most zoos indicates that fasting days are not used as part of a concept that tries to mimic the gorge-fast rhythms in natural habitats, because there is neither a widespread emphasis on increasing the amount of food nor the amount of physical exercise and cognitive challenge on the day before fasting. Few studies have investigated the effects, finding changes in energy intake and body condition due to the change in the total amount fed per week, while from the behavioral perspective, changes differed between studies, likely due to additional details such as the time of the day food

was provided or animal group size and composition. In some cases, animals paced more when feeding happened in the afternoon, which was interpreted as an anticipatory behavior with animals perceiving cues that it was feeding day, while in other cases, they paced more on fasting days. It may be particularly challenging to combine gorge-feeding, which is mainly feasible when feeding large carcasses that are conveniently just placed in the enclosure, with physical and cognitive activity; this represents a major challenge and opportunity for innovative feeding methods, and an important next step in large carnivore husbandry (Kleinlugtenbelt, 2023).

Another study published in the same journal, conducted by Anouk Frens and Marcus Clauss, addresses an additional well-known fact: large carnivores do not have 100% hunting success. This means that when they are motivated to feed, they cannot always satisfy that need instantly and must try repeatedly. For example, leopards have a hunting success rate of only 20%, while lions achieve a success rate of 29%. These numbers are specific to the ecological context of the observed populations and can vary based on season, prey availability, and likely predator experience. To the authors' knowledge, this concept has not yet been replicated in zoo settings, where animals are typically guaranteed food regardless of whether access is easy or difficult. The idea of failing to obtain food, the cognitive incentive to focus, and the potential feeling of success that might come with securing the prey have not been thoroughly studied in relation to predator behavior and welfare in zoos (Fens and Clauss, Journal of zoo and aquarium research, 2024). Clauss and Schiffmann (2022) propose that the opportunity for failure may represent an important aspect of a "meaningful" life for these animals, as an intuitive concept. One of the few examples of a device in zoos that simulates this idea is a moving bait zip-line for cheetahs *(Acinonyx Jubatus)*, which pulls up the prey after a short period during which it is within reach of the animals (Fig. 8). However, this study does not thoroughly explain the overall feeding strategy, such as whether a "failed attempt" means a fasting day or if the animals eventually receive the food later.

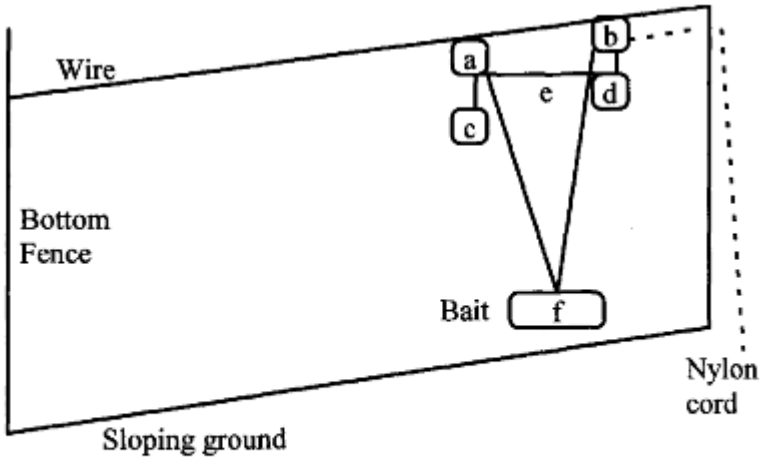


Fig. 8. Schematic diagram of the enrichment device within the enclosure: a= bottom pulley, b= top pulley, c= steel counter weight, d= lightweight, e= steel wire, f= dead rabbit (Williams et al., 1996)

Designing hygienic, escape-proof and technically feasible ways to present carnivores with their food, in a manner that allows them to occasionally fail in obtaining it, could be another promising direction for future carnivore husbandry (Fens and Clauss, Journal of zoo and aquarium research, 2024).

Overall, in the future, zoo management should aim to integrate feeding practices that consider the full spectrum of carnivore behavior, with a strong emphasis on reducing stress and promoting enrichment during all phases of their feeding cycle.

6. CONCLUSIONS

This thesis explored various welfare management practices for wild cats in captivity, focusing on different nutrition strategies and the associated challenges and benefits.

Whole prey plays a significant role in replicating natural behaviors and ensuring the physical and psychological well-being of these animals. Offering carcasses helps maintain a balanced diet, providing essential nutrients and promoting natural chewing and consumption patterns. Additionally, it encourages natural foraging behaviors, which are crucial for reducing stress and stereotypies. The inclusion of fur and feathers, as part of whole prey, also benefits the gastrointestinal health of felines by promoting healthy digestion and preventing issues like constipation.

However, this approach comes with challenges. Sourcing, preparing and storing carcasses can be difficult and requires careful management to avoid risks such spoilage, pathogens, and choking hazards. Furthermore, not all carnivores respond equally to this practice, and while some species benefit, others may experience behavioral changes, such as the increased pacing in tigers.

Ethical considerations are also an important part, with strict guidelines in place to ensure that feeder animals are sourced responsibly and humanely. Public perception remains a concern, but studies have shown that many zoo visitors understand the importance of these nutritional strategies for the health and enrichment of the animals.

Lastly, while specific feeding schedules, such as fasting days, are commonly implemented and aim to replicate natural feeding patterns and prevent obesity, their effectiveness in zoos remains uncertain. More research is needed to explore alternative methods that address both physical and cognitive needs in order to better simulate wilderness and enhance the welfare of captive wild cats.

7. BIBLIOGRAPHY

Bashaw, M. J., Bloomsmith, M. A., Marr, M. J., & Maple, T. L. (2003). To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biology*, *22*(2), 189–198. https://doi.org/10.1002/zoo.10065

Buchini, J. L. C. C., & Gobetti, S. T. d. C. (2021). Food management of wild cats in captivity. *International Journal of Development Research*, *11*(01), 43484–43488. Retrieved from https://www.journalijdr.com/sites/default/files/issue-pdf/20756.pdf

Carbone, C., Teacher, A., & Rowcliffe, J. M. (2007). The costs of carnivory. *PLoS Biology*, *5*(2), Article e22. https://doi.org/10.1371/journal.pbio.0050022

C. De la Fuente, M. F., Souto, A., B. Caselli, C., & Schiel, N. (2017). People's perception on animal welfare: Why does it matter? *Ethnobiology and Conservation*, 1–7. https://doi.org/10.15451/ec2017-10-6.18-1-7

De Cuyper, A., Clauss, M., Hesta, M., & Janssens, G. P. (2015). Feeding strategies in wild carnivores: Progress report of a model approach. *Nutrition Advisory Group to the Association of Zoos and Aquariums*, 3. Retrieved from https://nagonline.net/3988/feeding-strategies-wild-carnivores-progress-report-model-approach/

Depauw, S., Hesta, M., Whitehouse-Tedd, K., Vanhaecke, L., Verbrugghe, A., & Janssens, G. P. J. (2011). Animal fibre: The forgotten nutrient in strict carnivores? First insights in the cheetah. *Journal of Animal Physiology and Animal Nutrition*, *97*(1), 146–154. https://doi.org/10.1111/j.1439-0396.2011.01252.x

Dierenfeld, E. S. (1997). Captive wild animal nutrition: A historical perspective. *Proceedings of the Nutrition Society*, *56*(3), 989–999. https://doi.org/10.1079/pns19970104

Dierenfeld, E. S., Alcorn, H. L., & Jacobsen, K. L. (2002). Nutrient composition of whole vertebrate prey (excluding fish) fed in zoos. *Beltsville, Md. : U.S. Dept. Of Agriculture, Agricultural Research Service, National Agricultural Library, Animal Welfare Information Center*, *7994*. Retrieved from https://www.researchgate.net/publication/251886278_Nutrient_Composition_of_Whole_Vertebrate_Prey_Excluding_Fish_Fed_in_Zoos

EAZA standards for welfare, accommodation and management of animals in zoos and aquariums. (2024). (p. 38). Amsterdam: European Association of Zoos and Aquaria (EAZA). Retrieved from https://strapi.eaza.net/uploads/2024_04_WAM_Standards_Approved_06a0df2fe8.pdf

Edwards, M. S. (2014, February 10). Role of nutrition programs in zoological institutions • AZA Nutrition Advisory Group. Retrieved from https://nagonline.net/1379/role-nutrition-programs-zoological-institutions/

Enemark, L., Clauss, M., Lagerström, L., Burkevica, A., Gustafsson, J., Johnsson, J., Lundgren, P., & L. H. Rhode, H. (2023). The behavioural effects of feeding lean meat vs whole rabbit carcasses to zoo jaguars Panthera onca.

Journal of Zoo and Aquarium Research, *11*(3), 324–328. https://doi.org/10.19227/jzar.v11i3.730

Escobar-Ibarra, I., Mota-Rojas, D., Gual-Sill, F., Sánchez, C. R., Baschetto, F., & Alonso-Spilsbury, M. (2021). Conservation, animal behaviour, and human-animal relationship in zoos. Why is animal welfare so important? *Journal of Animal Behaviour and Biometeorology*, *9*(1), 1–33. https://doi.org/10.31893/jabb.21011

Fabretti, A. K., Gomes, L. A., Kemper, D. A. G., Chaves, R. O., Kemper, B., & Pereira, P. M. (2020). Clinical determination of the nutritional status of companion animals. *Semina: Ciências Agrárias*, *42*(5), 1813–1830. https://doi.org/10.5433/1679-0359.2020v41n5p1813

Finch, K., Williams, L., & Holmes, L. (2020). Using longitudinal data to evaluate the behavioural impact of a switch to carcass feeding on an Asiatic lion (Panthera leo persica). *Journal of Zoo and Aquarium Research*, *8*(4), 283–287. https://doi.org/10.19227/jzar.v8i4.475

Frens, A., & Clauss, M. (2024). Nutrition as an integral part of behavioural management of zoo animals. *Journal of Zoo and Aquarium Research*, *12*(4), 196–204. Retrieved from https://jzar.org/jzar/article/view/786

Greene, B. D. (2022). Feline diet. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior* (pp. 2675–2680). Springer Nature Switzerland AG. Retrieved from https://link.springer.com/referenceworkentry/10.1007/978-3-319-55065-7_1751#citeas

Hartstone-Rose, A., Selvey, H., Villari, J. R., Atwell, M., & Schmidt, T. (2014). The three-dimensional morphological effects of captivity. *PLoS ONE*, *9*(11), Article e113437. https://doi.org/10.1371/journal.pone.0113437

Holliday, J. A., & Steppan, S. J. (2004). Evolution of hypercarnivory: The effect of specialization on morphological and taxonomic diversity. *Paleobiology*, *30*(1), 108–128. https://doi.org/10.1666/0094-8373(2004)030%3C0108:eohteo%3E2.0.co;2

Kerr, K. R. (2012). Nutritional evaluation of raw meat and whole prey diets for domestic and exotic cats. Dissertation. Urbana-Champaign: University of Illinois. Retrieved from https://www.ideals.illinois.edu/items/32326

Kim, S., Cho, Y. S., Kim, H.-M., Chung, O., Kim, H., Jho, S., . . . Yeo, J.-H. (2016). Comparison of carnivore, omnivore, and herbivore mammalian genomes with a new leopard assembly. *Genome Biology*, *17*(1). https://doi.org/10.1186/s13059-016-1071-4

Kleinlugtenbelt, C. L. M. (2023). Large carnivore husbandry in European zoos. Dissertation (monographical). Zurich: University of Zurich, Vetsuisse Faculty. Retrieved from https://www.zora.uzh.ch/id/eprint/234361/

Kleinlugtenbelt, C., Clauss, M., Burkevica, A., & De Cuyper, A. (2023). Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry. *Journal of Zoo and Aquarium Research*, *11*(3), 318–323. https://doi.org/10.19227/jzar.v11i3.713

Krafte Holland, K., Larson, L. R., & Powell, R. B. (2018). Characterizing conflict between humans and big cats Panthera spp: A systematic review of research trends and management opportunities. *Plos One*, *13*(9), Article e0203877. https://doi.org/10.1371/journal.pone.0203877

Lamberski, N. (2015). Felidae. In R. E. Miller & M. E. Fowler (Eds.), *Fowler's zoo and wild animal medicine, volume 8* (pp. 467–476). Elsevier. Retrieved from https://pmc.ncbi.nlm.nih.gov/articles/PMC7152389/

Mcphee, M. E. (2002). Intact carcasses as enrichment for large felids: Effects on on- and off-exhibit behaviors. *Zoo Biology*, *21*(1), 37–47. https://doi.org/10.1002/zoo.10033

Mellor, D. J., Hunt, S., & Gusset, M. (Eds.). (2015). *Caring for wildlife: The world zoo and aquarium animal welfare strategy*. Gland, Switzerland: World Association of Zoos and Aquariums (WAZA) Executive Office. Retrieved from https://www.waza.org/wp-content/uploads/2019/03/WAZA-Animal-Welfare-Strategy-2015_Portrait.pdf

Mellen, J. D. (1997). Minimum husbandry guidelines for mammals: Small felids. american association of zoos and aquariums. *Nutrition Advisory Group to the Association of Zoos and Aquariums*, 6. Retrieved from https://nagonline.net/763/zoo-standards-keeping-small-felids-captivity/

NAG carcass feeding statement. (2013, December 30). Nutrition Advisory Group to the Association of Zoos and Aquaria. https://nagonline.net/663/nag-carcass-feeding-statement/

Guidelines for the humane and ethical acquisition and management of vertebrate feeder animals (excluding fish). (2017, October 27). Nutrition Advisory Group to the Association of Zoos and Aquaria. https://nagonline.net/5889/heamvfa/

Nijboer, J. (2020). Nutrition in zoo carnivores - management and nutrition - MSD veterinary manual. Retrieved from https://www.msdvetmanual.com/management-and-nutrition/nutrition-exotic-and-zoo-animals/nutrition-in-zoo-carnivores

Roth, E. K., Visscher, N. C., & Robinette Ha, R. (2017). Food for thought: Assessing visitor comfort and attitudes toward carcass feeding at the ABQ biopark zoo. Anthrozoös, 30(2), 227–235. https://doi.org/10.1080/08927936.2017.1310987

Shoemaker, A. H., Maruska, E. J., & Rockwell, R. (1997). Minimum husbandry guidelines for mammals: Large felids american association of zoos and aquariums. *Nutrition Advisory Group to the Association of Zoos and Aquariums*, 5. Retrieved from https://nagonline.net/761/zoo-guidelines-keeping-large-felids-captivity/

Shukla, M., Pandey, A., & Pandey, Y. (2014). Wild animals in captivity with special reference to carnivore health. *Veterinary Science Research Journal*, *5*(1and2), 50–53. https://doi.org/10.15740/has/vsrj/5.1and2/50-53

Skibiel, A. L., Trevino, H. S., & Naugher, K. (2007). Comparison of several types of enrichment for captive felids. *Zoo Biology*, *26*(5), 371–381. https://doi.org/10.1002/zoo.20147

Sutherland, W. J., Dicks, L. V., Petrovan, S. O., & Smith, R. K. (2021). Management of captive animals. *What Works in Conservation*, *6*, 527–553. https://doi.org/10.11647/OBP.0267

Whitehouse-Tedd, K. M., Lefebvre, S. L., & Janssens, G. P. J. (2015). Dietary factors associated with faecal consistency and other indicators of

gastrointestinal health in the captive cheetah (acinonyx jubatus). *Plos One*, *10*(4), Article e0120903. https://doi.org/10.1371/journal.pone.0120903

Wildon, A., & Kleyn, R. (2014, April 10). The nutritionist's role in the management and care of captive wild animals | spesfeed. Retrieved from https://spesfeed.com/2014/04/the-nutritionists-role-in-the-management-and-care-of-captive-wild-animals/

Our approach to animal welfare - WAZA. (2020). Retrieved from https://www.waza.org/priorities/waza-code-of-ethics/our-approach-to-animal-welfare/#:~:text=WAZA's%20Approach%20to%20Animal%20Welfare&text=The%20ability%20to%20have%20species,Council%20on%208%20October%202020.

Williams, B., Kay Waran, N., Carruthers, J., & John Young, R. (1996). The effect of A moving bait on the behaviour of captive cheetahs (acinonyx jubatus). *Animal Welfare*, *5*(3), 271–281. https://www.cambridge.org/core/journals/animal-welfare/article/abs/effect-of-a-moving-bait-on-the-behaviour-of-captive-cheetahs-acinonyx-jubatus/FCC5920759A51EE147602A00C50BDBD6

8. ACKNOWLEDGEMENTS

To my parents and my brother for their sacrifices, to everybody who rooted for me: I love you.