Department for Small Animals, Clinic for Zoo Animals, Exotic Pets and Wildlife

of the Vetsuisse Faculty University of Zurich

Director Head of Institution: Prof. Dr. med. vet. Jean-Michel Hatt

Work under the academic supervision of

Prof. Dr. med. vet. Marcus Clauss

Large Carnivore Husbandry in European Zoos

Inaugural-Dissertation

to obtain the title of Doctor from the

Vetsuisse Faculty University of Zurich

submitted by

Cellina Lucia Maria Kleinlugtenbelt

Veterinarian

from Baden-Baden, Germany

Approved at the request of

Prof. Dr. med vet Marcus Clauss, Referent

2023

Table of content

Zusammenfassung

Vetsuisse-Fakultät-Universität Zürich (2023)

Cellina Lucia Maria Kleinlugtenbelt

Klinik für Zoo-, Heim-, und Wildtiere, zootierklinik@vetclinics.uzh.ch

Große Karnivoren Haltung in Europäischen Zoos

Die Lebenserwartung von Raubtieren in Zoos ist gestiegen, aber wie wird diese längere Lebenszeit verbracht? Da die Fütterung Einfluss auf das Verhalten von Raubtieren haben kann, haben wir die Fütterungsroutinen in 44 europäischen Zoos in 7 verschiedenen Ländern durch persönliche Besuche erfasst und die Haltungsrichtlinien für 11 verschiedene Großraubtierarten untersucht. Während dieser Besuche bewerteten wir die aktuelle Fütterung in den Zoos und die Körperkondition mit Hilfe eines standardisierten Scores (BCS 1-9), von einem einzigen Beobachter angewendet. Die meisten Zoos steigerten die Futtermenge vor einem Fastentag nicht, im Einklang mit Haltungsempfehlungen, aber im Widerspruch zur Biologie. Als Futtermittel wurde in den meisten Zoos Fleisch am Knochen verwendet; Ganzkörper wurden hauptsächlich von Kleintieren, nicht aber von grösseren Tieren verfüttert. Während viele Einrichtungen über ein Repertoire an Fütterungsmethoden mit unterschiedlichem potenziellen Bereicherungswert berichteten, verwendeten die meisten während der Besuche diejenigen Methoden, die als wenig arbeitsintensiv und wenig kognitiv bereichernd einzustufen sind. Der BCS war bei den meisten Arten um den "idealen" Wert von 5 normalverteilt, mit einer leichten Verschiebung zu höheren BCS. Die derzeitigen Fütterungsmethoden von Zoo-Raubtieren sollten überdacht werden, um den Beschäftigungswert zu steigern. Insbesondere grosse Ganzkörper mit herausfordernder Darreichung sollten häufiger eingesetzt werden.

Keywords: große Fleischfresser, Fütterungsmethoden, Ganzkörper-Fütterungen, animal fiber, gorge-fast regime

Summary

Vetsuisse-Fakulty-University Zurich (2023)

Cellina Lucia Maria Kleinlugtenbelt

Clinic for Zoo Animals, Exotic Pets and Wildlife, zooklinik@access.uzh.ch

Large Carnivore Husbandry in European Zoos

While zoo carnivore life expectancy has increased, the question remains how these longer lives are spent. Because feeding management may particularly influence carnivore behaviour, we collected and recorded feeding routines in 44 European zoos in 7 different countries by personal visits and surveyed husbandry guidelines for 11 different large carnivore species. During these visits, we assessed the current feeding situation in zoos and the body condition using a standardized body condition score (ranging from 1-9) applied by a single investigator. Most zoos did not include a gorge-feeding day prior to the fasting days, in accord with guidelines but in contrast to biological logic. As diet items, meat on bone was used by the majority of zoos, and carcass feeding was mainly practiced with small, but hardly with large carcasses. Whereas many facilities reported a certain repertoire of feeding methods of varying potential enrichment value, during the visits themselves, most facilities used those methods of their feeding repertoire that can be considered less labour-intensive and less enriching. For most species, the BCS showed a close to normal distribution around the 'ideal' score of 5, with a slight shift towards higher BCS. We suggest that current feeding regimes of zoo carnivores should be re-assessed to increase the behavioural value of feeding. Feeding methods employing large carcasses presented in ways that make access labour-intensive should become more frequently used.

KEYWORDS: large carnivores, feeding methods, whole carcass, animal fiber, gorge-fast regime

Publication note

Large carnivore feeding in European zoos

Accepted for publication

Journal: Der Zoologische Garten N.F.

Journal of Zoo And Aquarium Research

Large carnivore feeding in European zoos

Cellina L. M. Kleinlugtenbelt[1], Anita Burkevica[2], Marcus Clauss[1]

[1] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich,

Winterthurerstr. 260, 8057 Zurich, Switzerland

[2] Parken Zoo, Flackstavägen 13, 63222 Eskilstuna, Sweden

Cellina L. M. Kleinlugtenbelt: cellinaluciamaria.kleinlugtenbelt@uzh.ch 0000-0002-7073-3547
Anita Burkevica: anita.burkevica@parkenzoo.se
Marcus Clauss: mclauss@vetclinics.uzh.ch 0000-0003-3841-6207

Correspondence to: Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife,

Vetsuisse Faculty, University Zurich, Winterthurerstr 260, 8057 Zurich, Switzerland

Abstract

While zoo carnivore life expectancy has increased, the question remains how these longer lives are spent. Because feeding management may particularly influence carnivore behaviour, we collected and recorded feeding routines in 44 European zoos in 7 different countries by personal visits. During these visits, we assessed the current feeding situation in zoos, which was achieved by following the responsible staff members on their daily routines with 11 different carnivore species. Meat on bone as a diet item was used by the majority of zoos, and carcass feeding was mainly practiced with small (rodents, rabbit, chicken), but hardly with large carcasses. Whereas many facilities reported a certain repertoire of feeding methods of varying potential enrichment value, during the visits themselves, most facilities used those methods of their feeding repertoire that can be considered less labour-intensive and less enriching. The number of facilities that only used a limited number of feeding methods was unexpectedly high, and methods like swing pole feeder, pulley feeders or self-serving feeders were not in use in any visited facility. Additionally, neither methods that require social carnivores to cooperate to access food, nor other feeding methods during which animals can actually fail to obtain their food (mimicking unsuccessful hunting) were reported. We suggest that in order to more closely mimic natural conditions and possibly enhance carnivore welfare, large carcass feeding in physically and cognitively challenging ways should be used more frequently, with a written feeding management plan to ensure that these feeding methods are not only used sporadically, but at a consistent frequency. Such an approach could at the same time ensure that appropriate resources in terms of equipment, diet items, and work time are available.

Key words: carnivores, feeding methods, feeding enrichment, pole feeding, whole carcass, bungee carcass, animal fibre

Introduction

In zoos worldwide, carnivore neonate mortality has decreased and adult carnivore longevity has increased over the decades (Roller et al. 2021). While this is a positive development, it is nevertheless necessary to monitor how these longer lives are spent by the animals. Carnivore husbandry has been particularly criticized in terms of behavioural deficits (Clubb and Mason 2003, 2007; Kroshko et al. 2016). While these may not represent threats to survival, they may compromise animal welfare.

Feeding is an important part of zoo animal management. Evidently the dietary regime must provide the animals with the energy and nutrients required for optimal health. This does not only imply an appropriate provision with proteins, fats, minerals, and vitamins, but also with less easily digestible material. In carnivores, these represent, on the one hand, physically challenging components required for dental health, such as the prevention of dental calculus (Bond and Lindburg 1990; Roe and Cleave 2005). Studies have also shown that animals fed whole-prey items vs. those fed processed meat suffered fewer gingival health problems, less plaque formation, and less focal palatine erosion (Lindburg 1988). On the other hand, less digestible material represents substrates summarized as 'animal fibre', i.e., bones, tendons, cartilage, skin, hair, and feathers including collagens, glycosaminoglycans and keratin (Depauw et al. 2012; Depauw et al. 2013). These substrates have fermentation properties that lead to specific conditions in the hindgut; in particular, they may temper the negative side effects of protein fermentation into putrefactive compounds (Depauw et al. 2012; Depauw et al. 2013). Whole prey is considered to provide an appropriate and balanced proportion of 'animal fibre' in comparison to pure meat, because of these less fermentable substances (Depauw et al. 2012; Depauw et al. 2013). Free-ranging carnivores use variable feeding strategies (De Cuyper et al. 2018); carnivores hunting comparatively small prey typically ingest the whole prey animal, whereas carnivores that hunt large prey may – especially during periods of plentiful prey presence – decide to only ingest the more digestible parts. Therefore, actual 'animal fibre' intake in natural habitats may be particularly variable for large-prey predators.

Furthermore, feeding has important consequences for behaviour. The ease with which animals can ingest their food, and the ease with which they can obtain it, defines the occupational value provided by that food. For example, a portion of minced meat will require less time of appetitive behaviour than a similar amount of whole meat that requires more complex oral processing. Similar differences will occur when feeding whole meat with and without bone, or pieces of a carcass with or without skin and fur, or whole carcasses with or without the digestive tract. Veninga and Lemon (2001) found that a pack of African wild dogs required a much longer feeding time for a whole carcass (60 minutes) as compared to a similar amount of pieced meat (3 minutes). For cheetahs, Bond and Lindburg (1990) reported improved appetites, longer feeding bouts, and a greater possessiveness of food in animals that were carcass-fed. For social carnivores, large carcass feeding has been suggested to have positive effects on social cohesion (Macdonald 1996; Höttges et al. 2019). Therefore, the use of whole prey feeding has been advocated from a behavioural point of view. Table 1 gives an overview over typical diet items used in carnivore feeding.

Similarly, different ways exist that make the obtaining of the food a more complex procedure. Evidently, a lump of minced meat put in front of the animal requires less time for acquisition than the same amount of minced meat distributed across various locations within the enclosure. Spreading the provided food over different locations, either by hiding, scatter feeding, or by making small amounts available from feeders at regular or irregular intervals, is a simple way of increasing the occupational value of the food (Table 2). This is particularly appropriate for animals consuming small prey items, but less feasible for animals feeding on larger items. For animals of the latter group, a variety of methods have been proposed to make access to diet items more challenging, some of which can also be used to make access to a single small diet item more challenging for small-prey feeders (Table 3).

Table 1. Typical diet items used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these diet items were personally observed during the survey visit.

Item	Description	Reported in zoos	of which personally observed
Minced / Processed meat	Meat and similar products, made into a relatively homogenous mass that has a dough-like consistency and little physical structure, often supplemented with essential nutrients – mainly commercially available products, which may come as raw meat, heat-processed moist (mainly canned) food, or dry (mainly extrudates)	2%	0%
Commercial preparations	Commercially available food, such as dog/cat/ zoo carnivore dry and wet foods and pellets (especially for bears)	30%	38%
Organs	Any kind of organ whole or chopped up	45%	20%
Whole meat	Cuts of meat in various sizes (from golf ball size to several kilograms) – mainly from large (prey*) animals	55%	42%
Meat on bone	Meat pieces still connected to the bone – mainly from large (prey*) animals	98%	72%
Whole meat with fur/feathers	Cuts of meat with skin and fur still attached but no bone – mainly from large (prey*) animals	23%	10%
Carcass parts with fur/feathers	Carcass parts with meat attached to bone, skin and fur still attached (e.g., ¼ deer carcass cut up) – mainly from large (prey*) animals	57%	12%
½ carcass	½ carcass with skin and fur intact and red organs still inside the carcass – mainly from large (prey*) animals	30%	15%
Complete eviscerated carcass	Carcass without any organs – large or small prey*	0%	0%
Carcass without digestive tract	Carcass without intestines, but still with red organs – large or small prey*	30%	15%
Decapitated carcass	Carcass without head – large or small prey*	20%	22%
Whole carcass	Complete carcass unopened or with abdomen opened – large or small prey*	95%	38%

*'prey' includes domestic animals; large prey examples are cattle, sheep, goats, deer, horses, donkeys, or zoo hoof stock; small prey examples are rodents, rabbits, juvenile or adult poultry, or zoo rodents

Table 2. Feeding options used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these feeding options were personally observed during the survey visit.

Option	Description	Example references	Reported in zoos	of which personally observed
One portion (per animal)	One pile of food in the enclosure easily accessible for the animal		100%	80%
Group feeding	Animals are fed in a group with whole carcass to share among them		NA	NA
Scattering	Pieces of the offered food scattered around the enclosure	(Law et al. 1997; Andrews and Ha 2014)	68%	47%
Hiding	Hiding the food within the enclosure	(Fischbacher and Schmid 1999)	64%	68%
Time-delayed dispensing	The food is distributed or dispensed at various (non-random or random) times during the day	(Shepherdson et al. 1989; Carlstead et al. 1991; Fischbacher and Schmid 1999)	9%	25%

NA not assessed in the present study

Table 3. Feeding Methods used in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use in which these feeding methods were personally observed during the survey visit

Method	**Description**	**References**	**Reported in zoos**	**of which personally observed**
Hand feeding	Food is provided with long tweezers directly into the mouth of the individual		11%	80%
Loose on the ground	Food is either thrown in, placed on the ground of the enclosure or in a food dish		100%	93%
Tied to the ground	Food is tied to objects such as trees, rocks on the ground level		59%	35%
Hung up	Food is hung up on any available place in the enclosure		84%	46%
Hung up with counterweight	Food is hung up with a weight on the opposite site of a rope, which pulls the food back up as soon as released	(Law et al. 1997)	2%	0%
Hung up with option of being pulled at the opposite site	Food is hung up with the option of being pulled against at the opposite		2%	0
Hung up elastic cord	Food attached to elastic cord dangling over ground	(O'Neal 2011)	25%	9%
Swinging platform	Moving platform off ground under hanging food	(Hare and Jones 2018)	5%	50%
Woodpile feeder	Food under branches piled together	(Law et al. 1997)	2%	100%
Feeding stick	Food stuck to a stick hung from some high point; animal must cling to stick while getting food off	(Law et al. 1997)	2%	0%
Swing pole feeder	Box with a whole at the base bolted to the roof, access via a swinging pole underneath it to which the animal must cling	(Law et al. 1997)	0%	0%
Self-serving feeder	Individuals can get food by themselves from certain objects in their enclosure	(Law et al. 1997; Gusset et al. 2002; Andrews and Ha 2014)	0%	0%
Movement induced dispenser	Object with holes, comes in all different shapes, and sizes which releases food when moved around	(Law and Kitchener 2002; Law and Reid 2010; Hare and Jones 2018)	16%	0%
Pole feeding	Wooden pole with food at the top	(Law et al. 1997)	20%	44%
Run	Lure system to stimulate the hunting instinct	(Quirke et al. 2013; Fischer et al. 2021)	5%	0%
Zipline feeding	Zip line within the enclosure incl. a device to connect food, can move forwards and backwards along the line		18%	50%
Pulley feeder	Zipline connected with fire hose, food attached to a track runner out of reach	(Hare and Jones 2018)	0%	0%
Novel objects / self built	Novel objects either self built or commercially purchased		16%	57%
Dug in ground	Food dug into the ground at different depths		16%	14%
Swimming	Food presented in different locations, for the animals only to be reached while swimming		23%	20%

Hand feeding means the animals receive their meals in mouth-sized pieces by a long tweezer directly into their mouth. If food is provided **loose on the ground**, the food will either be thrown in, placed on the ground of the enclosure, or in a food dish. The meals can also be **tied to the ground** with the help of a carabiner in stones, logs**,** or other objects within the enclosure. The animal must pull the meat off to access its meal or eat at the fixed spot.

Hanging up food on ropes or carabiners in different heights is a widely used method in any carnivore (Fig. 1A) and can be combined with any enclosure structure so that the animal has to first climb to the spot where the food is hung. To make it more challenging, a weight can be attached to the other side of the rope so if the food is let go, it will be pulled back up and the individual must begin from the start; alternatively, similar constructions can facilitate that another animal, a keeper or visitors pull at the other side of the rope (Fig. 1B). O'Neal (2011) describes the use of **carcass hanging on an elastic cord** in Tasmanian devils (*Sarcophilus harrisii)*, where the carcass is secured to a bungee cord that is attached to the fort in the devils' enclosure, and left dangling above the ground. This should increase effort for food acquisition, and promotes behaviours strengthening muscles necessary for social feeding and carcass tearing. A **swing-pole feeder** is a container with a hole cut in the base which can be fixed to the roof inside the enclosure. A free-swinging branch attached to the underside of the roof provides access to the container. The cats climb onto the branch and thrust their paws through the opening to reach the food (Law et al. 1997). **Feeding sticks** involve wooden stick-like objects which can be fitted with simple wooden spigots at one end and hooks at the other. The stick can be repositioned for each feed so that the cat does not have easy access to it by means of an adjacent branch but must put some effort into obtaining the food. Cats will leap from the floor and cling onto the stick, supporting their body weight, while fighting to free the food from the wooden spigot (Law et al. 1997). On other occasions, the food may be procured by springing from the nearest log onto the stick after exploring which launch point is nearest to the stick (Law et al. 1997).

The **feeding pole** consists of a wooden pole or tree (Fig. 1D), which can variate in height, with e.g. a loose-fitting wooden spigot hammered into the top (Law et al. 1997). The food item, such as part of a horse or cow leg, is hung on the peg. The original publication suggests that only one animal should have access to the pole at a time to avoid rivalry, but since its appearance, several facilities have successfully used several poles for the corresponding number of animals simultaneously. The carnivore climbs up the pole, grabs the food, and climbs or jumps back down (Law et al. 1997). Felids use the same muscles when climbing trees as they do when grappling with and pulling down a large prey animal, such as a wild Water buffalo (*Bubalus arnee*) or Sambar (*Rusa unicolor*) (Turner and Anton 2000). Therefore, climbing a pole to access food provides a realistic simulation of the physical activity required by big cats when they hunt (Law and Kitchener 2019).

Swinging food platforms are suspended off the ground by a wire cable at each of the corners. The meat is attached to a rope or bungee cord directly above the platform, so the individual has to stand up on the moving platform, balancing while trying to remove the meat from the cord (Hare and Jones 2018) (Fig. 1C).

A specialized lure system often called the '**cheetah run'** has been adopted at various institutions worldwide to simulate the instinctual chase for the cheetah and serve as an enriching activity, which can also be used for other species (Fischer et al. 2021). Animals are trained to chase the lure and receive a reward after the completion (Quirke et al. 2013; EAZA 2018). A different variant of the lure chasing system is a food chasing system which works the same way but instead of getting a reward after the completion, the individuals chase after their meal portion which will be received at the successful 'hunt'. Some may use a similar system to the one used for coursing greyhounds, which consists of a car starter motor operated by a hand held trigger switch, a string with a lure, is powered by a car battery, and pulleys are used in order to set out the course of the lure (Quirke et al. 2013).

Ziplines can be easily constructed by a metal rope attached on both ends inside the enclosure; with a carabiner or a roll construction, food can be attached to the zipline and will move back and forth if the animal is trying to pull it off. The **pulley feeder** is a zip line design to promote cooperative physical exercise for animals that hunt in a group, e.g., African hunting dogs (*Lycaon pictus*) (Hare and Jones 2018). Ideally set on a hillside enclosure the meat is attached to a track runner and when resting at the bottom of the slope it is out of reach for the pack. A strip of fire hose or rope dangling from the runner must be used to drag the meat back up the hill, pull it down, and hold it in place while others feed (Hare and Jones 2018). Similar setups, which have apparently not been used widely for other purposes than research, allow access to food only when at least two animals cooperate, e.g. when pulling at the same time at different ropes (Drea and Carter 2009; Marshall-Pescini et al. 2017; Borrego 2020) (Fig. A1).

Woodpile feeders are branches piled together which provide a complex lattice in which food can be hidden. These feeders increase the effort and time spent searching for food (Law et al. 1997).

Furthermore, **electronic feeders** can be used in all carnivores. A sufficient amount of food will be distributed to the feeding box, which will be closed by a sliding door with a strong magnet (Jenny and Schmid 2002). When the magnet is turned on the animal cannot open the door. Each magnet can be switched off during certain periods of time, randomly spread over the day, which happens without any associated noise (Jenny and Schmid 2002). Electronic feeders are available in all different shapes and sizes, such as the electronic scatter feeders, which are placed above the ground and scatter certain foods, e.g. pellets for bears randomly throughout the day (Andrews and Ha 2014). **Self-serving feeders** are available in various options. The main concept is that the individuals can feed whenever they want from a certain amount of food placed in the self-serving feeder, which will fill up whenever emptied. This mechanism permits a continuous supply of e.g. pellets for bears but prevents them from spilling or playing with the food (Ziegltrum and Nolte 1997).

Movement-induced dispensers range from balls to barrels; basically, holes can be put into anything. They all work with the same principle: food will fall out as soon as the object containing it is moved around. The dispensers can either be left on the ground or hung up. Different constructions such as the 'wobble tree' are also available for the use in bears, where food is placed in a container on top of a long flexible pole, which is too thick for breaking and too smooth for climbing; to obtain the food the bear must shake it free (Law and Kitchener 2002).

However, the methods mentioned above are not the only ones existing. Motivated, engaged people can create their own methods, with few limits set to the imagination on how to feed carnivores in a more challenging way. The overall objective of the present study was to collect data on the variety of frequently used feeding methods and used food items for large carnivores in a variety of European zoos. The ultimate goal of this paper is to provide animal care professionals in zoos a potential framework to explore, evaluate and also get new ideas on how to feed captive large carnivores.

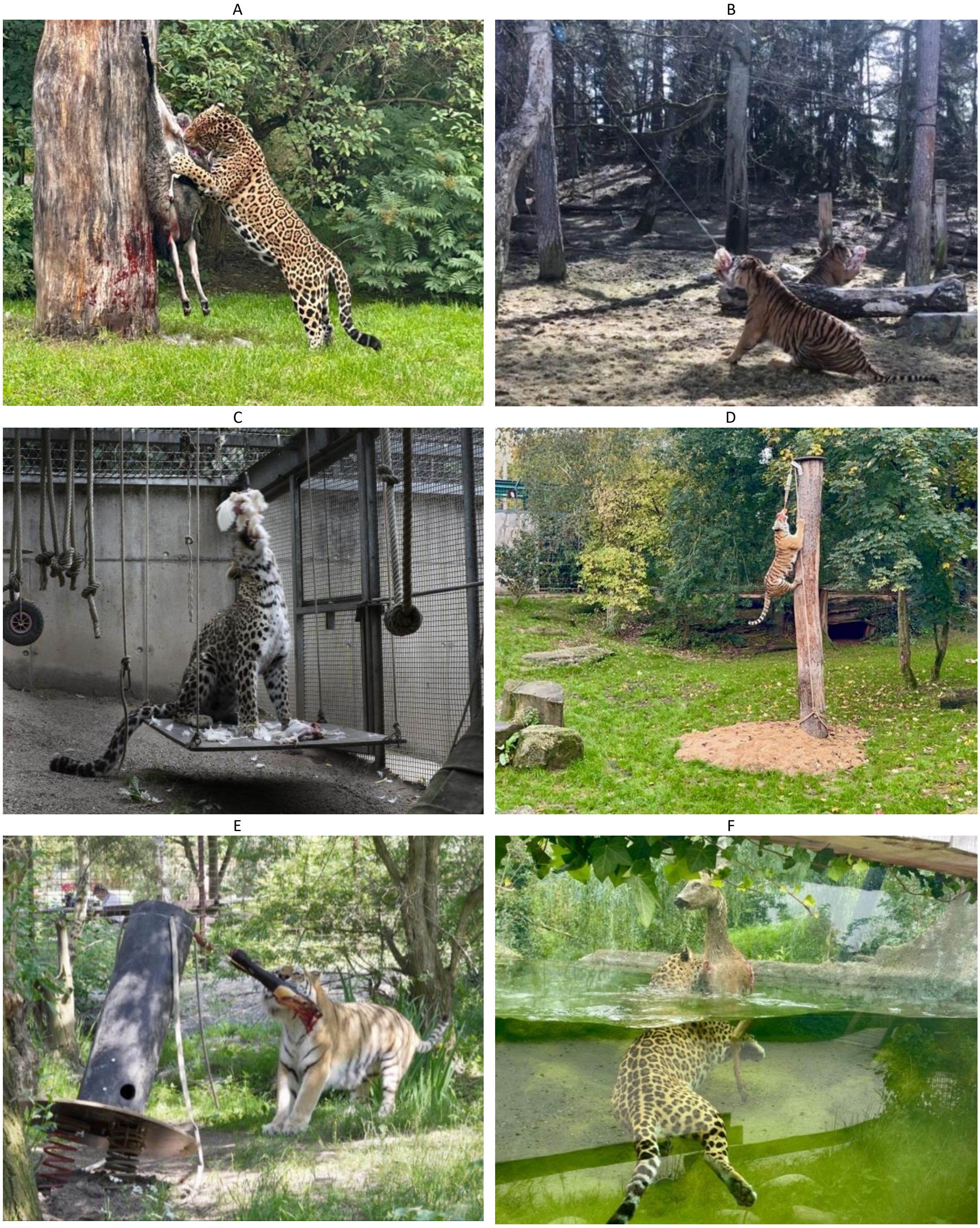

Figure 1. Examples of different feeding methods for large carnivores: (A) carcass tied to a tree, Parken Zoo, Sweden; (B) counter-pulling system for two animals, Parken Zoo, Sweden; (C) swinging platform – Cologne Zoo, Germany; (D) pole feeding, Cologne Zoo, Germany; (E) self-built feeding object, Odense 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.

Methods

This study was conducted with the support of the EAZA Felid TAG and Canid and Hyeanid TAG. We collected and compiled data from 44 zoos in 7 countries by personal visits of the first author; one zoo sent their information in since a personal visit was not possible due to COVID-19 restrictions. Thus, we observed 69 tigers (*Panthera tigris*) (26 zoos), 119 lions (*Panthera leo*) (31 zoos), 16 jaguars (*Panthera onca*) (7 zoos), 28 leopards (*Panthera pardus*) (15 zoos), 27 snow leopards (*Panthera uncia*) (13 zoos), 55 cheetahs (*Acinonynx jubatus*) (15 zoos), 40 lynxes (*Lynx lynx*) (16 zoos), 27 hyenas (*Crocuta crocuta and Hyaena hyaena*) (11 zoos), 75 wolves (*Canis lupus*) (16 zoos), 66 brown bears (*Ursus arctos*, including one brown bear – polar bear hybrid) (15 zoos), and 36 polar bears (*Ursus maritimus*) (12 zoos) during their feeding to see which feeding methods are used, how they are applied and how the animals react to them. This was done by following the responsible staff members on their daily routines with the selected species, both from behind the scenes and from the point of view of a visitor. During personal interviews with the responsible staff members, we gained more information about used feeding options, whether the animals interact with them, and how they are approached. The interview was based on a pre-planned set of questions but was conducted as a free-flowing conversation rather than a structured ticking off from the individual questions. All interviews were conducted by the first author. Feeding was documented with photos and videos. The interview included details about the used diet items, feeding options and frequently used methods. We divided the results into two types: what was stated during the interviews, and what was observed during the actual feeding by the first author during the visit. Some feedings could not be observed in person due to the presence of newborn, the separation of diseased individuals, the current hygienic rules at a zoo due to the current COVID-19 outbreak, and current hibernation of several bears.

The diet items, feeding types and feeding methods were defined as in Tables 1-3.

Results

The information obtained and the observations made during the visits are given on a species basis in Tables A1-A11 in the appendix. Here, we mention the major findings.

Diet items (Table 1)

Meat on bone was used by the majority of zoos for most of the species with a percentage of 98% closely followed by **whole carcass** with 95%. With a lesser frequency, the use of **carcass parts with fur or feathers** still attached (57%), **whole meat** (55%) and **organs** (45%) was reported. At a lower frequency, 30% of zoos used **commercial preparations** as part of their diet plan, **½ carcass** or **carcass without the digestive tract**. 23% used **whole meat with fur or feathers** still attached and 20% **decapitated** their **whole carcasses** before feeding them to their carnivores. **Minced and processed meat** with 2% and **complete eviscerated carcasses** with 0% were used the least in all species.

Whole carcass use was reported in 94% of lynxes, 91% of hyenas, 87% of leopards, 85% of tigers, 84% of lions, 81% of wolves, 77% of snow leopards, 73% of cheetahs, 71% of jaguars, 50% of polar bears and 47% of brown bears. It was less frequently personally observed during the visit - in 5 out of 15 zoos that stated the use for their lynxes, 3/10 for hyenas, 6/13 for leopards, 3/22 for tigers, 2/26 for lions, 2/13 for wolves 4/10 for snow leopards, 4/11 for cheetahs, and 2/5 for jaguars. In none of the zoos were bears fed whole carcass during our visits due to the reduced feeding in the autumn and winter periods.

When splitting the reported use of carcasses by the size of the carcass (large carcass: considered everything as big as a goat or bigger, incl. juvenile goats/sheep older than 4 months; small carcass: everything up to the size of a goat, incl. juvenile goat/sheep up to 4 months), a distinct difference was evident (Fig. 2, Table 4). Large carcasses were used very rarely by the surveyed zoos; only 2 zoo used large carcasses on a weekly basis. The majority of zoos did not use large carcasses at all, or only very sporadically (Fig. 2A). By contrast, small carcasses were frequently used, with a large majority of zoos using them at least once per week (Fig. 2B).

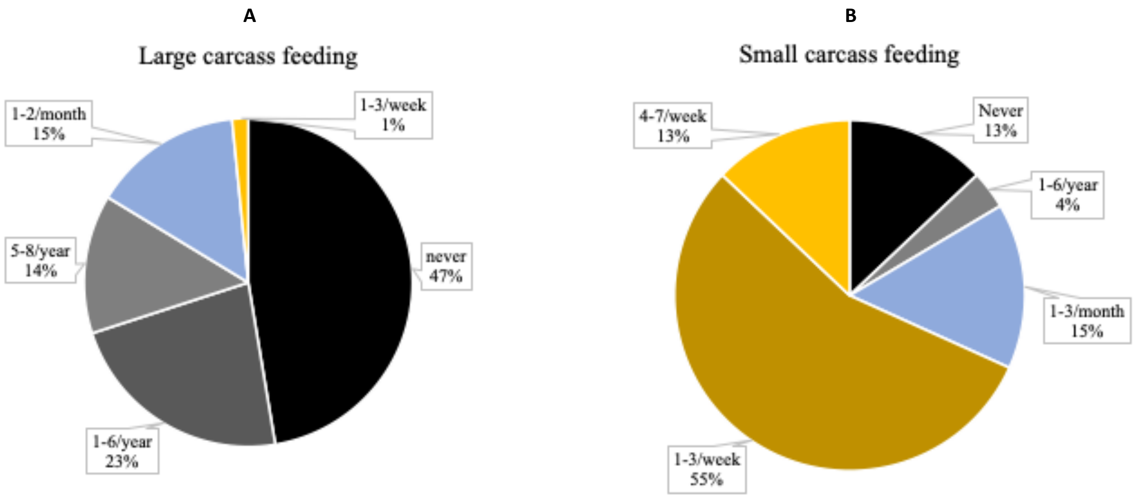

Figure 2 Summary of the use of (A) large and (B) small carcass feeding for 11 species of large carnivores in 44 European zoos

Although not quantified in the present study, interviews often suggested that the responsibility for choosing a diet item can differ: it may lie with the zoo commissary or a person higher up the zoo hierarchy than the keepers, and more rarely with the keepers themselves.

Table 4. Overview of the frequency of large and small carcass use in feeding of zoo carnivores, their reported use in the 44 European zoos that participated in the present study, and the percentage of those zoos that reported their use.

	tiger	lion	jaguar	leopard	snow leopard	cheetah	lynx	hyena	wolf	brown bear	polar bear
					Large carcass feeding						
never	9 (35%)	7 (23%)	5 (71%)	9 (60%)	6 (46%)	11 (73%)	13 (81%)	8 (73%)	2 (13%)	10 (67%)	10 (83%)
1-6/year	4 (15%)	6 (19%)	1 (14%)	3 (20%)	4 (31%)	1 (7%)	1 (6%)	-	2 (13%)	1 (7%)	2 (17%)
5-8/year	5 (19%)	7 (23%)	1 (14%)	-	2 (15%)	2 (13%)	1 (6%)	1 (9%)	4 (25%)	3 (20%)	-
1-2/month	7 (27%)	10 (32%)	-	2 (13%)	1 (8%)	1 (7%)	1 (6%)	2 (18%)	3 (19%)	1 (7%)	-
1-3/week	-	1 (3%)	-	-	-	-	-	-	1 (6%)	-	-
					Small carcass feeding						
never	1 (4%)	-	-	-	-	1 (7%)	1 (6%)	2 (18%)	3 (19%)	8 (53%)	6 (50%)
1-6/year	1 (4%)	2 (6%)	-	1 (7%)	1 (8%)	-	-	-	-	1 (7%)	-
1-3/month	6 (23%)	7 (23%)	3 (43%)	1 (7%)	2 (15%)	1 (7%)	1 (6%)	1 (9%)	2 (13%)	-	3 (25%)
1-3/week	14 (54%)	20 (65%)	4 (57%)	9 (60%)	6 (46%)	9 (60%)	11 (69%)	8 (73%)	6 (38%)	5 (33%)	2 (17%)
4-7/week	2 (8%)	-	-	4 (27%)	4 (31%)	4 (27%)	3 (19%)	-	2 (13%)	1 (7%)	2 (17%)

Feeding option

The option of feeding **one portion** for each animal was used the most with 100% of all visited zoos reporting it. Unfortunately, **group feeding** was not systematically included in the questionnaire, but it can be expected that wherever large whole carcasses are fed, it most likely is for a group to share. This method was personally observed in two zoos. **Scattering** the food was reported by 68% of zoos with the majority scattering for brown bears (67%), 64% used **hiding** the food within the enclosure, e.g., in novel objects and 9% indicated the use of **time-delayed dispensing** at various random and non-random times during the day. The latter method was reported the most in polar bears with 17%, 0% used this method in cheetahs, lynxes, hyenas and wolves.

During the personal visits, one portion-feeding was observed in 80% of zoos that reported its use, hiding was observed in 68% of zoos that reported its use and scattering and time-delayed dispensing in 47% and 25% of the zoos reporting the respective use.

In many cases, keepers mentioned that it was their own responsibility to choose a feeding option. In the case of mechanical dispensers, it was stated repeatedly that the use of these machines was dependent on their maintenance and state of functioning. No written instructions on the use or frequency of feeding options were indicated.

Feeding method

All of the zoos reported placing **food loose on the ground (including platforms)**, e.g., in a pile**,** which was practiced in 100% of leopards, snow leopards, cheetahs, hyenas, and polar bears but only in 60% of brown bears. 84% of zoos reported **hanging up food**; this was only reported in 20% of brown bears but 86% of jaguars. 59% reported **tying** the meal **to the ground** with a majority using this method in their tigers (69%), 25% **hung it up attached to a bungee cord,** 20% used a **pole feeding** method of which 15% used it for tigers and 43% for jaguars. 18% indicated the use of a **zipline** construction, 16% a **movement-induced dispenser**, 11% **handfed** their carnivores, 5% used a **run** and another 5 % a **swinging platform**. The swinging platform was only used in leopards. 2% **hung the food up with a counterweight** or used a **woodpile feeder** or a **feeding stick,** and no facility used a **swing pole feeder**, **self-serving feeder,** or **pulley feeder.**

Observations on the day of visit were: **loose on the ground** - 93% of the zoos that reported its use, hand feedings - 80%, **swinging platforms** and **ziplines** - 50%, **hanging** the

meal up – 46%, **pole feedings** - 44%, **tied to the ground** - 35%, hanging on an **elastic cord** - 9%, **counterweight hanging up**, **feeding sticks**, **movement induced dispensers** and **run constructions** - 0%.

In addition to the methods listed in Table 3, various **self-built** options and novel objects were in use. 16% of the zoos built several options themselves (e.g., Fig. 1E), of which 31% were zoos with tigers and 25% with polar bears. These methods were observed in 57% of the zoos that reported their use. 16% of zoos reported **hiding the food being dug into the ground** for the animals to find, mainly in hyenas (36%). This was observed in 14% of the zoos reporting this use. 23% reported presenting the food **on or in water,** mainly for polar bears (30%). This was observed in 20% of the zoos reporting this use. One zoo practiced hanging a carcass over water for jaguars, who thus had to detach the carcass while swimming (Fig. 1D). Across all species, half of the zoos either used only loose on the ground and hand feeding or one additional method (Table 5).

Table 5. Quantity of additional feeding methods excluding hand feeding and placing food loosely on the ground

Species	Zoos using additional methods to feeding loose on the ground and hand feeding							
	0	1	2	3	4	5	6	7
Tiger	1 (4%)	3 (12%)	4 (15%)	8 (31%)	6 (23%)	1 (4%)	3 (12%)	0 (0%)
Lion	6 (19%)	7 (23%)	6(19%)	5 (16%)	5 (16%)	1 (3%)	1 (3%)	0 (0%)
Jaguar	0 (0%)	2 (29%)	1 (14%)	2 (29%)	1 (14%)	1 (14%)	0 (0%)	0 (0%)
Leopard	3 (20%)	3 (20%)	5 (33%)	3 (20%)	0 (0%)	1 (7%)	0 (0%)	0 (0%)
Snow Leopard	3 (23%)	3 (23%)	4 (31%)	2 (15%)	1 (8%)	0 (0%)	0 (0%)	0 (0%)
Cheetah	8 (53%)	5 (33%)	0 (0%)	2 (13%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Lynx	5 (31%)	5 (31%)	2 (13%)	2 (13%)	0 (0%)	0 (0%)	2 (13%)	0 (0%)
Hyena	5 (45%)	1 (9%)	4 (36%)	1 (9%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Wolf	10 (63%)	2 (13%)	1 (6%)	2 (13%)	1 (6%)	0 (0%)	0 (0%)	0 (0%)
Brown bear	3 (20%)	4 (27%)	2 (13%)	2 (13%)	2 (13%)	0 (0%)	1 (7%)	1 (7%)
Polar bear	4 (33%)	3 (25%)	2 (17%)	2 (17%)	0 (0%)	0 (0%)	1 (8%)	0 (0%)
average (%)	28%	22%	18%	17%	7%	3%	4%	1%

Subjectively the speed of consuming the meal was faster when feeding by hand or placing the meal loose on the ground without any obstacle compared to any other discussed feeding method such as pole feeding and bungee cord feeding.

Although not quantified in the present study, interviews mainly did not point out a person responsible for the choice of, or the frequency of use of, feeding methods. No written instructions on the use or frequency of feeding methods were indicated; however, in individual cases, an unwritten, clear concept of this frequency was evident during the interviews.

Discussion

In this study we recorded, in person, the current situation of large carnivore feeding methods in European zoos for different large carnivore species managed at 44 facilities, to record the status quo on the variety and frequency of food items and feeding methods in use. The information obtained indicates that a variety of diet items and methods are in the repertoire of the zoological institutions visited.

Free-living carnivores are able to perform appetitive behaviours – looking for prey, stalking, capturing, killing and processing. These behaviours are typically not successful each time they are executed; for example, van Orsdol (1984) reported hunting success of lions in Uganda varying between 27 and 34%. In contrast, these behaviours have been described as permanently not occurring in managed environments like zoos (with the possible exception of processing in the case of whole carcass feeding); the ensuing frustration and behaviour regulation dysfunction has been suggested to contribute to stereotypies (Jenny and Schmid 2002). To have animals work for their food in a cognitive challenging but also biologically appropriate way can provide animals with an opportunity for learning and remembering relevant skills that help them control their ability to access and procure food (Meehan and Mench 2007). Complex, challenging feeding methods can be seen, proactively, as a way to offer positive welfare; alternatively, they can be seen, reactively, as a preventative or curative measure against behavioral indicators of negative welfare (Wagman et al. 2018). The viewpoint – proactive or reactive – may depend on the individual facility's self-understanding as an institution dedicated to creating naturalistic husbandry environments, or as an institution operating under historical burdens that affect husbandry.

In the present study, several observations stood out: (i) The low frequency of large carcass feeding; (ii) that during the visits themselves, mostly those methods of the facilities' repertoires were used that can be considered less labour-intensive and less enriching; (iii) the high number of facilities that only used a very limited number of feeding methods; and (Miller et al.) that none of the visited zoos used written protocols that defined the frequency of use for the different feeding methods.

Limitations of this study

Several limitations of the present study need to be mentioned. The number of zoological institutions was, at 44, low compared to the overall number of zoos existing in

Europe. Theoretically, a larger number of facilities could have been included by using a questionnaire approach, but our focus was on personal visits that, in the experience of the senior author, often better reflect husbandry reality, and may also lead to insights that cannot be gleaned from survey answers. The COVID pandemic limited the visit options in the time window available for the study.

The potentially most important limitation was the time available for the zoo personnel during the visit. Given that the interview, including the visitation of the facilities, introduction to the animals, the preparation of the food most likely represented an additional time expense on the part of the zookeepers, it may be understandable that in order to compensate, the more labour-intensive feeding methods were not used during the visit. Alternatively, one might have expected that the visits – which were announced well in advance and coordinated with the zoological institution to accommodate to the disposability of the carnivore staff – might have been an incentive to show off the more elaborate feeding methods available. Either way, it remains difficult to interpret the observation that in the majority of cases, the more labour-intensive feeding methods were not employed. Nevertheless, this finding emphasizes that on average, these methods have not become part of the invariable routine in the participating zoos but are still being employed on a more selective basis. Yet, some zoos include these methods in their daily routines to the extent that the reported more complicated feeding options were actually used, also on the day of visit.

A topic that was left out deliberately in the present study was the question where the responsibility lay for diets chosen, feeding methods available at the facility, and actually use of feeding methods. We expected little gain in results that ascribe this responsibility to certain members of the zoo team (like 'the keepers', 'the curators', 'the commissary personnel', the veterinarians'), and suspected that this would vary between facilities. We had the impression of a trend that the diet items used were decided by groups different from the keepers, and that the daily use of a feeding method was more in the realm of keepers' decisions. However, in the case of intended adjustments to a current dietary regime, every group would have to work cooperatively to define a new goal and put it into practice.

A topic not included in the present study was the use of so called "medical feeding", where animals need to be fed several times a day to receive their drugs within the food.

Diet items: large carcass feeding

The historical approach to carnivore feeding was the provision of meat, which needs to be supplemented to avoid evident deficiencies such as calcium deficiency (Allen et al. 1996). Actually, minced meat products, fully supplemented, are used for large carnivore feeding in zoos (Allen et al. 1996; Young 1997), but these feeds appear to be less popular among European zoos, including the ones of the present study. The necessity of supplementing such a diet with bones for dental health is well known, as is the lack of stimulus they provide for the cranial musculature (Young 1997). As an evident alternative to adding supplements and structural components to a (minced) meat diet, whole prey feeding has been promoted as well, since it is considered to provide an appropriate and balanced proportion of 'animal fibre' in comparison to pure meat, because of less fermentable substances, such as bones, tendons, cartilage, skin, hair, and feathers (Depauw et al. 2012; Depauw et al. 2013).

Research on the effects of whole-prey feeding is still limited, but the general current impression is that it is considered beneficial in physiological and behavioural terms (Bond and Lindburg 1990; McPhee 2002; Cloutier and Packard 2014). For example, Wood and Norris (2000) underlined the importance of recognizing that physical forms of foods greatly influence the feeding behaviour of captive carnivores. This psychological benefit of a natural diet cannot be imitated or even duplicated with a processed diet form (Roe and Cleave 2005). Whole prey closely resembles the natural diet of carnivores, even if differences in the body composition of wild prey and domestic animals – which typically represent the source for whole prey – are well-documented (Veninga and Lemon 2001; McPhee 2002; Gaengler and Clum 2015). The documentation of such differences should not lead to the conclusion that they are so large as to make domestic animals an unsuitable food for zoo carnivores; anyhow, the main other options of carnivore feeding are also based on domestic animal products.

Whole prey feeding might be a valuable contribution to a nature-oriented carnivore husbandry. The structure, texture and palatability of whole carcass feeding does encourage various natural behaviors and therefore helps avoiding monotony (Roe and Cleave 2005). One aspect of large carcass feeding that should be further investigated is its effect on group behaviour. Large carcass feeding may lead to agonistic interactions between group members all feeding on the large carcass, and fear of such conflicts may be one reason why some zoo managers do not want to include it in the feeding regime. However, assuming that social tensions will require an outlet, Höttges et al. (2019) suggested that a large carcass provides such an outlet in a specific situation. Resolving social tensions in a feeding context may lead to less conflict at other times where no additional motivation (feeding) might temper the encounter. In anthropocentric terms, large carcass feeding might offer a comparatively safe stage for solving social conflicts.

Given the relevance of large carcasses for large carnivores, one might assume that anyone – from visitors to animal managers – knowledgeable about the natural feeding behaviour of large carnivores would intuitively understand the value of large, whole carcass feeding. Nevertheless, large carcasses were used very rarely in the zoos that participated in the present study. We could not quantify reasons for this remarkable finding. On the one hand, these may lie in the additional logistic effort required to acquire large carcasses (Allen et al. 1996) and to clean enclosures after large carcass feeding (Young 1997). On the other hand, they may lie in a real or assumed unease of zoo visitors with large carcass feeding. It is difficult to judge how justified this perception is. Actually, several studies performed in different countries showed that zoo visitors are not generally opposed to carcass feeding, and actually perceive it as valuable for the animals and believe that there is also an educational value in feeding whole carcass (Veninga and Lemon 2001; Gaengler and Clum 2015; Roth et al. 2017 incl. several unpublished studies). In some human societies, there probably is a cognitive dissociation, or the lack of an association, between the practice to consume meat and the killing of animals that is a prerogative for that practice. While there may be reasons to cherish an absence of a conscious condoning of killing in terms of our human civilization, this dissociation appears difficult to reconcile with the mission of nature education, and concepts of sustainability, which are based on an accountability for our actions. Given its combined effect of nutritional value, behavioural management, and public education, the general lack of large carcass feeding is one of the surprising findings of the present study. The fact that large carcass feeding represents a physical challenge for commissary personnel and keepers means that decisions to promote this feeding need to be flanked by measures that make large carcass feeding logistically feasible.

Finally, large carcass feeding is most likely linked to an alternating feeding and fasting regime (Kleinlugtenbelt et al. subm). Apart from representing the natural biology of the species and the corresponding behavioural, physiological and educational effects, variation between individual days might enhance visitor frequency given that there may be an incentive to observe the other day’s condition.

Large carnivore feeding methods

The easiest, least time-consuming method (simply placing the meal inside the enclosure on the ground or throwing the portions over the fence) was the most used one during the visits to the facilities. As a slight modification of this method, tying the food to the ground, or hanging it from some enclosure structure, was widely used (Table 3 & A5-11). While arguably being cognitively more stimulating than food put loosely on the ground, most of the observations indicated that it took the individual animals very little time (typically, less than 2 minutes), to both get to the location where the food could be reached, and to pull it off its attachment. The same might apply for other methods that fasten the food to a certain location and just make the attainment of that location particularly challenging, including pole feeding, bungee carcasses or zip line feeding. In these scenarios, major effects – when comparing to the current baseline situation – most likely could already be attained by attaching the food more tightly, so that the attachment represents a true physical challenge rather than a negligible obstacle. Fastening the food to specific locations in the enclosure can provide variety in itself, if the different possible areas in the enclosure represent different physical challenges.

The various self-built options observed in this study that have, to our knowledge, not been widely described in the literature, bespeak considerable motivation and engagement to make feeding a challenging moment for zoo carnivores. On the other hand, the low use or lack of use of swing pole feeders, self-serving feeders or pulley feeders indicate that the published repertoire of feeding methods was not fully used by the participating facilities. In particular, the lack of feeding methods that require cooperation of social carnivores (Drea and Carter 2009; Marshall-Pescini et al. 2017; Hare and Jones 2018; Borrego 2020), appears as a lost opportunity, both in terms of the attractivity and educative potential of exhibits and in terms of effects on the social cohesion of the animal group (Fig. A1).

Arguably, the most important feature of a planned feeding regime is the variety of methods employed. In this respect, some facilities excelled, in particular for tigers, lions, lynx or brown bears (Table 5). On the other hand, the repertoire of methods available for cheetah or wolves appeared particularly limited. Potentially, due to the anatomy of their forelimbs, these species are intuitively considered less suitable for feeding methods that require grabbing food with piercing claws and with paws in supination. Averaged across all species, 50% of facilities employed feeding on the ground/by hand only or one additional method (Table 5). Although to our knowledge studies are lacking, we consider it a well-founded intuition that an increasing number of feeding methods will foster the physical and cognitive development of zoo carnivores. At the same time, it might again enhance the attractivity of enclosures for visitors and even incite more frequent visits. If visitors witness a pole feeding, for example, but also learn that at other times, a swinging platform feeding, a run, or a carcass hung above water might be used, they might want to witness these other methods as well. Including a variety of feeding options in the enclosure design and the management of the species may represent good husbandry practices. Evidently, sufficient work time and a consistent maintenance of the respective constructions must be factored into these plans.

A variety of feeding options might open yet another opportunity for behavioural management of zoo animals. Animals can be trained to associate certain signals with specific events. Most commonly, this occurs even involuntarily, leading to typical patterns of anticipatory behaviour once specific cues have been perceived, including time of day in regular management schedules, or sounds, looks or smells associated with food delivery. These anticipatory behaviours need not necessarily be considered negative (Watters 2014). Actually, a study with dolphins (*Tursiops truncatus*) indicated that the degree of anticipatory behaviour can be interpreted a measure for how much animals want to participate in a certain situation, with dolphins showing more anticipatory movement when perceiving the signal that a human would play with them compared to a signal that toys would be provided within the next half hour (Clegg et al. 2018). Transferring these observations to large carnivores, it appears plausible that once the animals have learned to associate a certain signal with a certain feeding methods (e.g, pole feeding, pulley feeder, run), they would anticipate the feeding event, which might represent a valuable cognitive enrichment for the time until feeding takes place.

In order to ensure that challenging feeding methods are not only used sporadically, but at a consistent (yet possibly randomly varying) frequency, it may be advisable to have a written management plan. Such an approach could at the same time ensure that appropriate resources in terms of equipment, diet items, and work time are available, and could serve to document the degree of husbandry engagement.

Outlook

One possibly crucial feature of natural food procurement that is lacking from feeding methods employed in zoos as outlined above is the possibility of failure – the equivalent of an unsuccessful hunting attempt. Arguably, the experience of failure, and the consequential awareness of the possibility of failure, results in a different state of mind compared to an individual that was never unsuccessful. Actually, one might argue that a 100% success rate is not success, but just a way things are – success can only exist in the face of potential failure. Therefore, denying animals the possibility of failure (as in an 'unsuccessful feeding attempt') might mean denying them the experience of success.

None of the visited facilities followed an outspoken strategy that included failure as an option, although some provided food in a way that required a multi-hour engagement of the animal for a successful acquisition of the food (e.g., Fig. 1F). This lack of a failure option finds its equivalent in the literature on zoo carnivore feeding. To our knowledge, the only published description of a feeding device that moves the food out of the reach of the animals if they are too slow is a pulley system designed for cheetahs (Williams et al. 1996). However, the authors did not explain whether the animals still received their food after a failed attempt, of if they were fasted for a relevant time period before the next feeding opportunity. Providing animals species-adequate physical and cognitive challenges, with a relevant failure feedback that is distinct yet not harmful, so that they are motivated to solve these challenges, could be the major future advancement of carnivore husbandry.

Acknowledgements

We thank the Felid, Canid and Hyanid TAGs for their support and sincerely thank all participating Zoos, Odense Zoo, Copenhagen Zoo, Randers Zoo, Scandinavian Wildlife Park, Givskud Zoo, Skærup Zoo, Borås Zoo, Orsa Predator Park, Kolmården, Parken Zoo, Skansen, Kristiansand Zoo, Rotterdam Zoo, Wildlands Adventure Zoo Emmen, Antwerpen Zoo, Zoo Planckendael, Bremerhaven Zoo, Wildlife Park Springe, Muenster Zoo, Wingst Forest Zoo, Dortmund Zoo, Krefeld Zoo, Zoom Gelsenkirchen Zoo, Cologne Zoo, Frankfurt Zoo, Neuwied Zoo, Heidelberg Zoo, Karlsruhe Zoo, Wilhelma Stuttgart, Munich Zoo, Nuremberg Zoo, Leipzig Zoo, Animal Park Berlin, Osnabrueck Zoo, Serengeti Park Hodenhagen, Hannover Zoo, Wuppertal Zoo, Schwerin Zoo, Basel Zoo, Animal Park Bern, Wildlife Park Zurich Langenberg, Walter Zoo, Wildlife Park Bruderhaus, Zurich Zoo, and their involved staff, for their time, hospitality and participation in this study.

References

Allen ME, Oftedal OT, Baer DJ (1996) The feeding and nutrition of carnivores. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S (eds) Wild mammals in captivity Principles and techniques. University of Chicago Press, Chicago, pp 139-147

Andrews NL, Ha JC (2014) The effects of automated scatter feeders on captive grizzly bear activity budgets. Journal of Applied Animal Welfare Science 17: 148-156

Bond JC, Lindburg DG (1990) Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic feeding program on oral health and psychological well-being. Applied Animal Behaviour Science 26: 373-382

Borrego N (2020) Socially tolerant lions (*Panthera leo*) solve a novel cooperative problem. Animal Cognition 23: 327-336

Carlstead K, Seidensticker J, Baldwin R (1991) Environmental enrichment for zoo bears. Zoo Biology 10: 3-16

Clegg IL, Rödel HG, Boivin X, Delfour F (2018) Looking forward to interacting with their caretakers: Dolphins' anticipatory behaviour indicates motivation to participate in specific events. Applied Animal Behaviour Science 202: 85-93

Cloutier TL, Packard JM (2014) Enrichment options for African painted dogs (*Lycaon pictus*). Zoo Biology 33: 475-480

Clubb R, Mason G (2003) Captivity effects on wide-ranging carnivores. Nature 425: 473-474

Clubb R, Mason G (2007) Natural behavioural biology as a risk factor in carnivore welfare: How analysing species differences could help zoos improve enclosures. Applied Animal Behaviour Science 102: 303-328

De Cuyper A, Clauss M, Carbone C, Codron D, Cools A, Hesta M, Janssens G (2018) Predator size and prey size–gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. Oikos 128:

Depauw S, Bosch G, Hesta M, Whitehouse-Tedd K, Hendriks W, Kaandorp J, Janssens G (2012) Fermentation of animal components in strict carnivores: A comparative study with cheetah fecal inoculum. Journal of animal science 90: 2540-2548

Depauw S, Hesta M, Whitehouse-Tedd K, Vanhaecke L, Verbrugghe A, Janssens G (2013) Animal fibre: The forgotten nutrient in strict carnivores? First insights in the cheetah. Journal of Animal Physiology and Animal Nutrition 97: 146-154

Drea CM, Carter AN (2009) Cooperative problem solving in a social carnivore. Animal Behaviour 78: 967-977

EAZA (2018) Best practice guidelines cheetah (*Acinonyx jubatus*). EAZA Executive Office, Amsterdam

Fischbacher M, Schmid H (1999) Feeding enrichment and stereotypic behavior in spectacled bears. Zoo Biology 18: 363-371

Fischer B, Flint M, Cole K, George KA (2021) Development of an evidence-based welfare approach for cheetahs (*Acinonyx jubatus*) under human care. Animal Welfare 30: 295-306

Gaengler H, Clum N (2015) Investigating the impact of large carcass feeding on the behavior of captive Andean condors (*Vultur gryphus*) and its perception by zoo visitors. Zoo Biology 34: 118-129
Gusset M, Burgener N, Schmid H (2002) Wirkung einer aktiven Futterbeschaffung mittels Futterkisten auf das stereotype Gehen und den Glukokotikoidspiegel von Margays, *Leopardus wiedii*, im Zürich Zoo. Der Zoologische Garten 72: 245-262
Hare VJ, Jones MK (2018) Enrichment for physical fitness: let's get physical. Proceeding of the International Congress of Zookeepers 18:
Höttges N, Hjelm M, Hård T, Laska M (2019) How does feeding regime affect behaviour and activity in captive African lions (*Panthera leo*)? Journal of Zoo and Aquarium Research 7: 117-125
Jenny S, Schmid H (2002) Effect of feeding boxes on the behavior of stereotyping amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland. Zoo Biology 21: 573-584
Kleinlugtenbelt CLM, Clauss M, Burkevica A, De Cuyper A (subm) Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry. Journal of Zoo and Aquarium Research:
Kroshko J, Clubb R, Harper L, Mellor E, Moehrenschlager A, Mason G (2016) Stereotypic route tracing in captive Carnivora is predicted by species-typical home range sizes and hunting styles. Animal Behaviour 117: 197-209
Law G, Macdonald A, Reid A (1997) Dispelling some common misconceptions about the keeping of felids in captivity. International Zoo Yearbook 35: 197-207
Law G, Kitchener A (2002) Simple enrichment techniques for bears, bats and elephants - untried and untested. International Zoo News 49: 4-12
Law G, Reid A (2010) Enriching the lives of bears in zoos. International Zoo Yearbook 44: 65-74
Law G, Kitchener AC (2019) Twenty years of the tiger feeding pole: review and recommendations. International Zoo Yearbook 54: 174-190
Lindburg DG (1988) Improving the feeding of captive felines through application of field data. Zoo Biology 7: 211-218
Macdonald DW (1996) Social behaviour of captive bush dogs (*Speothos venaticus*). Journal of Zoology 239: 525-543
Marshall-Pescini S, Schwarz JF, Kostelnik I, Virányi Z, Range F (2017) Importance of a species' socioecology: Wolves outperform dogs in a conspecific cooperation task. Proceedings of the National Academy of Sciences 114: 11793-11798
McPhee ME (2002) Intact carcasses as enrichment for large felids: Effects on on- and off-exhibit behaviors. Zoo Biology 21: 37-47
Meehan CL, Mench JA (2007) The challenge of challenge: can problem solving opportunities enhance animal welfare? Applied Animal Behaviour Science 102: 246-261
Miller LJ, Ivy JA, Vicino GA, Schork IG (2019) Impacts of natural history and exhibit factors on carnivore welfare. Journal of Applied Animal Welfare Science 22: 188-196
O'Neal T (2011) Animal enrichment strategies for promoting natural behaviors in captive populations of Tasmanian devils (*Sarcophilus harrisii*). Independent Study Project:
Quirke T, O'Riordan R, Davenport J (2013) A comparative study of the speeds attained by captive cheetahs during the enrichment practice of the "cheetah run". Zoo Biology 32: 490-496
Roe S, Cleave R (2005) Are we just feeding carnivores or are we providing enrichment as well? In: International Conference on Environmental Enrichment. Wildlife Conservation Society, New York

Roller M, Müller DWH, Bertelsen MF, Bingaman Lackey L, Hatt J-M, Clauss M (2021) The historical development of juvenile mortality and adult longevity in zoo-kept carnivores. Zoo Biology 40: 588-595
Roth EK, Visscher NC, Ha RR (2017) Food for thought: assessing visitor comfort and attitudes toward carcass feeding at the ABQ BioPark Zoo. Anthrozoös 30: 227-235
Shepherdson D, Brownback T, James A (1989) A mealworm dispenser for Slender-tailed meerkat (*Suricata suricatta*) at London Zoo. International Zoo Yearbook 28: 268-271
Turner A, Anton M (2000) The Big Cats and their fossil relatives: An illutrated guide to their evolution and natural history. Columbia University Press, New York
van Orsdol KG (1984) Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. African Journal of Ecology 22: 79-99
Veninga SA, Lemon J (2001) Whole carcass feeding as a source of behavioural enrichment for African wild dogs (*Lycaon pictus*) in captivity at Western Plains Zoo, Dubbo. In: http://wwwpainteddogconservationiinetnetau/news/whole-carcass-feeding-by-veninga-and-lemon-2001pdf
Wagman JD, Lukas KE, Dennis PM, Willis MA, Carroscia J, Gindlesperger C, Schook MW (2018) A work-for-food enrichment program increases exploration and decreases stereotypies in four species of bears. Zoo Biology 37: 3-15
Watters JV (2014) Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. Zoo Biology 33: 251-256
Williams BG, Waran NK, Carruthers J, Young RJ (1996) The effect of moving bait on the behaviour of captive cheetahs (*Acinonyx jubatus*). Animal Welfare 5: 271-281
Wood P, Norris K (2000) Guidelines for the housing and management of African painted dogs (*Lycaon pictus*) at Perth Zoo. In: Zoo P (ed) Exotic Mammal Section
Young RJ (1997) The importance of food presentation for animal welfare and conservation. Proceedings of the Nutrition Society 56: 1095-1104
Ziegltrum GJ, Nolte DL (1997) Black bear damage management in Washington State. Proceedings of the Eastern Wildlife Damage Management Conference 7: 104-107

Appendix

Table A1. Methods of tigers (*Panthera tigris*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 26 zoological institutions.

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	21	6 (29%)	Hand feeding	0	-
Organs	8	0 (0%)	Hiding	16	3 (19%)	Loose on the ground	20	11 (55%)
Whole meat	1	0 (0%)	Scattering	14	4 (29%)	Tied to the ground	18	3 (17%)
Meat on bone	26	18 (69%)	Time-delayed dispensing	2	0 (0%)	Hung up	21	7 (33%)
Whole meat with fur/feathers	0	-				Hung up with counterweight	1	0 (0%)
Carcass parts with fur/feathers	12	3 (25%)				Hung up elastic cord	8	0 (0%)
1/2 carcass	11	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	1	1 (100%)
Carcass without digestive tract	4	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	7	0 (0%)				Self-serving feeder	1	0 (0%)
Whole carcass	22	3 (14%)				Movement induced dispenser	0	-
						Feeding stick	1	0 (0%)
						Pole feeding	4	1 (25%)
						Run	0	-
						Zip line feeding	5	1 (20%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	14	3 (21%)
						Novel objects / self built	8	2 (25%)
						Swimming	2	0 (0%)

Table A2. Methods of lions (*Panthera leo*) feeding in use, and personally observed, (incl. the % of institutions that reported the general use of the method), at 31 zoological institutions.

Diet item	use in number of zoos	personally observed (%facilities using method)	Feeding option	use in number of zoos	personally observed (%facilities using method)	Feeding method	use in number of zoos	personally observed (%facilities using method)
Minced/ processed meat	0	-	One pile for each	23	12 (52%)	Hand feeding	0	-
Organs	6	0 (0%)	Hiding	12	2 (17%)	Loose on the ground	30	12 (40%)
Whole meat	5	2 (40%)	Scattering	15	1 (7%)	Tied to the ground	18	4 (22%)
Meat on bone	31	18 (58%)	Time-delayed dispensing	1	0 (0%)	Hung up	22	4 (18%)
Whole meat with fur/feathers	10	3 (30%)				Hung up with counterweight	1	0 (0%)
Carcass parts with fur/feathers	11	0 (0%)				Hung up elastic cord	4	1 (25%)
1/2 carcass	9	2 (22%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	1	1 (100%)
Carcass without digestive tract	8	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	6	1 (17%)				Self-serving feeder	0	-
Whole carcass	26	2 (8%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	4	1 (25%)
						Run	0	-
						Zip line feeding	5	1 (20%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	11	1 (9%)
						Novel objects / self built	5	1 (20%)
						Swimming	0	-

Table A3. Methods of jaguars (*Panthera onca*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 7 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	2	0 (0%)	Hand feeding	0	-
Organs	1	0 (0%)	Hiding	2	2 (100%)	Loose on the ground	2	0 (0%)
Whole meat	2	0 (0%)	Scattering	2	0 (0%)	Tied to the ground	4	0 (0%)
Meat on bone	7	5 (71%)	Time-delayed dispensing	0	-	Hung up	6	4 (67%)
Whole meat with fur/feathers	0	-				Hung up with counterweight	0	-
Carcass parts with fur/feathers	3	2 (67%)				Hung up elastic cord	3	0 (0%)
1/2 carcass	1	1 (100%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	1	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	5	2 (40%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	3	1 (33%)
						Run	0	-
						Zip line feeding	1	1 (100%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	4	1 (25%)
						Novel objects / self built	1	1 (100%
						Swimming	1	1 (100%)

Table A4. Methods of leopards (*Panthera pardus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method) at 15 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	10	3 (30%)	Hand feeding	0	-
Organs	2	0 (0%)	Hiding	4	1 (25%)	Loose on the ground	15	7 (47%)
Whole meat	2	0 (0%)	Scattering	10	1 (10%)	Tied to the ground	6	0 (0%)
Meat on bone	15	12 (80%)	Time-delayed dispensing	0	-	Hung up	12	4 (33%)
Whole meat with fur/feathers	1	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	11	2 (18%)				Hung up elastic cord	2	0 (0%)
1/2 carcass	4	0 (0%)				Swinging platform	2	2 (100%)
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	13	6 (46%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	2	0 (0%)
						Run	0	-
						Zip line feeding	1	1 (100%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	5	0 (0%)
						Novel objects / self built	0	-
						Swimming	0	-

Table A5. Methods of snow leopards (*Panthera uncia*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 13 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	10	7 (70%)	Hand feeding	0	-
Organs	2	0 (0%)	Hiding	5	3 (60%)	Loose on the ground	13	7 (45%)
Whole meat	1	0 (0%)	Scattering	7	1 (14%)	Tied to the ground	5	0 (0%)
Meat on bone	13	8 (62%)	Time-delayed dispensing	1	0 (0%)	Hung up	9	2 (22%)
Whole meat with fur/feathers	7	1 (14%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	0	-				Hung up elastic cord	2	1 (50%)
1/2 carcass	3	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	1	0 (0%)				Self-serving feeder	0	-
Whole carcass	10	4 (40%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	0	-
						Pulley feeder	0	-
						Wrapped in something/ hidden	6	1 (17%)
						Novel objects / self built	0	-
						Swimming	0	-

Table A6. Methods of cheetahs (*Acinonynx jubatus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 15 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	14	12 (86%)	Hand feeding	1	1 (100%)
Organs	3	0 (0%)	Hiding	2	1 (50%)	Loose on the ground	15	12 (80%)
Whole meat	3	2 (67%)	Scattering	6	1 (17%)	Tied to the ground	2	0 (0%)
Meat on bone	13	4 (31%)	Time-delayed dispensing	0	-	Hung up	4	0 (0%)
Whole meat with fur/feathers	5	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	6	0 (0%)				Hung up elastic cord	1	0 (0%)
1/2 carcass	1	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	2 (67%)				Swing pole feeder	0	-
Decapitated carcass	2	0 (0%)				Self-serving feeder	0	-
Whole carcass	11	4 (36%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	3	0 (0%)
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	0	-
						Novel objects / self built	0	-
						Swimming	0	-

Table A7. Methods of lynxes (*Lynx lynx*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 16 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	16	13 (81%)	Hand feeding	2	1 (50%)
Organs	2	0 (0%)	Hiding	4	2 (50%)	Loose on the ground	15	11 (73%)
Whole meat	11	8 (73%)	Scattering	9	5 (56%)	Tied to the ground	4	0 (0%)
Meat on bone	10	6 (60%)	Time-delayed dispensing	0	-	Hung up	10	2 (20%)
Whole meat with fur/feathers	4	1 (25%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	4	0 (0%)				Hung up elastic cord	2	0 (0%)
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	3	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	15	5 (33%)				Movement induced dispenser	0	-
						Feeding stick	1	0 (0%)
						Pole feeding	3	2 (67%)
						Run	0	-
						Zip line feeding	3	2 (67%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	3	0 (0%)
						Novel objects / self built	2	2 (100%)
						Swimming	0	-

Table A8. Methods of hyenas (*Crocuta crocuta & Hyaena hyaena*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 11 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	11	3 (27%)	Hand feeding	1	1 (100%)
Organs	4	0 (0%)	Hiding	5	2 (40%)	Loose on the ground	11	7 (64%)
Whole meat	1	1 (100%)	Scattering	6	2 (33%)	Tied to the ground	3	0 (0%)
Meat on bone	11	7 (64%)	Time-delayed dispensing	0	-	Hung up	6	1 (17%)
Whole meat with fur/feathers	0	-				Hung up with counterweight	0	-
Carcass parts with fur/feathers	2	0 (0%)				Hung up elastic cord	0	-
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	0	-				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	10	3 (30%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	2	1 (50%)
						Novel objects / self built	0	-
						Digged in ground	4	1 (25%)
						Swimming	0	-

Table A9. Methods of wolves (*Canis lupus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 16 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	1	0 (0%)	One pile for each	14	2 (14%)	Hand feeding	1	1 (100%)
Organs	6	1 (17%)	Hiding	4	0 (0%)	Loose on the ground	14	7 (50%)
Whole meat	5	2 (40%)	Scattering	7	3 (43%)	Tied to the ground	4	1 (25%)
Meat on bone	12	2 (17%)	Time-delayed dispensing	0	-	Hung up	4	0 (0%)
Whole meat with fur/feathers	2	1 (50%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	7	0 (0%)				Hung up elastic cord	0	-
1/2 carcass	2	0 (0%)				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	2	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	0	-				Self-serving feeder	0	-
Whole carcass	13	2 (15%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	0	-
						Pulley feeder	0	-
						Wrapped in something/ hidden	3	0 (0%)
						Novel objects / self built	0	-
						Digged in ground	3	0 (0%)
						Swimming	0	-

Table A10. Methods of brown bears (*Ursus arctos*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 15 (11*) zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0 (0)	-	One pile for each	11 (10)	2 (20%)	Hand feeding	0 (0)	-
Organs	4 (2)	0 (0%)	Hiding	6 (6)	1 (17%)	Loose on the ground/ thrown in	15 (11)	7 (64%)
Whole meat	8 (7)	1 (14%)	Scattering	10 (7)	4 (57%)	Tied to the ground	6 (5)	0 (0%)
Meat on bone	11 (9)	1 (11%)	Time-delayed dispensing	1 (1)	0 (0%)	Hung up	8 (3)	0 (0%)
Whole meat with fur/feathers	3 (2)	0 (0%)				Hung up with counterweight	0 (0)	-
Carcass parts with fur/feathers	4 (4)	0 (0%)				Hung up elastic cord	0 (0)	-
1/2 carcass	0 (0)	-				Swinging platform	0 (0)	-
Complete eviscerated carcass	0 (0)	-				Woodpile feeder	0 (0)	-
Carcass without digestive tract	2 (1)	0 (0%)				Swing pole feeder	0 (0)	-
Decapitated carcass	2 (2)	0 (0%)				Self-serving feeder	0 (0)	-
Whole carcass	7 (6)	0 (0%)				Movement induced dispenser	7 (5)	0 (0%)
						Feeding stick	0 (0)	-
						Pole feeding	0 (0)	-
						Run	0 (0)	-
						Zip line feeding	0 (0)	-
						Pulley feeder	0 (0)	-
						Wrapped in something/ hidden	5 (2)	1 (50%)
						Novel objects / self built	1 (1)	1 (100%)
						Digged in ground	2 (1)	0 (0%)
						Swimming	6 (4)	1 (25%)

*Not counted are 4 institutions in which the bears were already hibernating

*In keepers' advice, bears should be slowed down in feeding enrichment towards the winter, therefore less different feeding methods could be personally observed, during autumn and winter

Table A11. Methods of polar bears (*Ursus maritimus*) feeding in use, and personally observed (incl. the % of institutions that reported the general use of the method), at 12 zoological institutions

Diet item	use in number of zoos	personally observed (% facilities using method)	Feeding option	use in number of zoos	personally observed (% facilities using method)	Feeding method	use in number of zoos	personally observed (% facilities using method)
Minced/ processed meat	0	-	One pile for each	12	5 (42%)	Hand feeding	4	4 (100%)
Organs	5	1 (20%)	Hiding	5	3 (60%)	Loose on the ground	12	6 (50%)
Whole meat	6	1 (17%)	Scattering	7	2 (29%)	Tied to the ground	2	0 (0%)
Meat on bone	7	1 (14%)	Time-delayed dispensing	2	0 (0%)	Hung up	5	0 (0%)
Whole meat with fur/feathers	1	0 (0%)				Hung up with counterweight	0	-
Carcass parts with fur/feathers	5	0 (0%)				Hung up elastic cord	1	0 (0%)
1/2 carcass	0	-				Swinging platform	0	-
Complete eviscerated carcass	0	-				Woodpile feeder	0	-
Carcass without digestive tract	1	0 (0%)				Swing pole feeder	0	-
Decapitated carcass	1	0 (0%)				Self-serving feeder	0	-
Whole carcass	6	0 (0%)				Movement induced dispenser	0	-
						Feeding stick	0	-
						Pole feeding	0	-
						Run	0	-
						Zip line feeding	1	0 (0%)
						Pulley feeder	0	-
						Wrapped in something/ hidden	1	1 (100%)
						Novel objects / self built	3	0 (0%)
						Digged in ground	0	-
						Swimming	3	1 (33%)

*In keepers' advice, bears should be slowed down in feeding enrichment towards the winter, therefore less different feeding methods could be personally observed, during autumn and winter

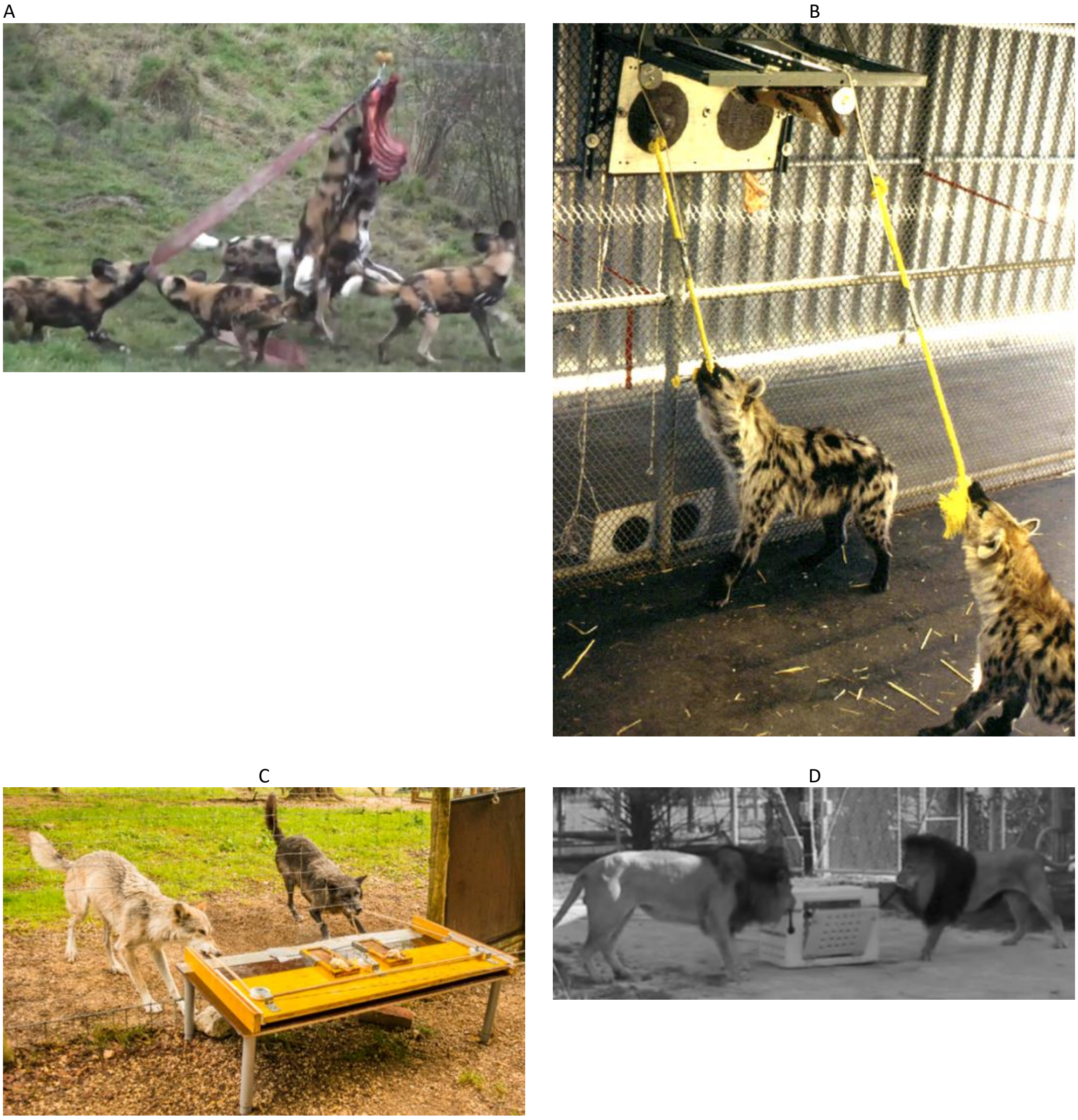

Figure A1. Examples of different feeding methods to display or test cooperative behaviour in large carnivores: (A) pulley feeder for cooperative canids, as described for African hunting dogs (*Lycaon pictus*) by (Hare and Jones 2018); screenshot from an uncredited video no longer available on youtube; (B) cooperation task in spotted hyenas (*Crocuta crocuta*); photograph from Drea and Carter (2009); (C) cooperation task in wolves (*Canis lupus*); photograph from Marshall-Pescini et al. (2017); (D) cooperation task in lions (*Panthera leo*); photograph from Borrego (2020).

Publication note

Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry

Accepted for publication

Journal: Journal of Zoo and Aquarium Research

JZAR JOURNAL OF ZOO AND AQUARIUM RESEARCH
www.jzar.org

JZAR Research article

OPEN ACCESS

Research article

Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry

Cellina L.M. Kleinlugtenbelt[1], Marcus Clauss[1], Anita Burkevica[2] and Annelies De Cuyper[3]

[1]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland
[2]Parken Zoo, Flackstavägen 13, 63222 Eskilstuna, Sweden
[3]Department of Veterinary and Biosciences, Faculty of Veterinary Medicine, Ghent, University, Heidestraat 19 9820 Merelbeke, Belgium

Correspondence: Marcus Clauss, email; mclauss@vetclinics.uzh.ch

Keywords: fasting days, gorge-fast regime, large carnivores

Article history:
Received: 3 Sep 2022
Accepted: 13 Apr 2023
Published online: 30 Apr 2023

Abstract

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. At the same time, there is a tradition of exposing these species to one or several fasting days per week in zoos. In this study husbandry guidelines for large carnivores were surveyed, and feeding routines recorded in 44 European zoos. Husbandry guidelines did not suggest that fasting days should be preceded by gorge-feeding, and the most common practice observed at the zoos also did not include a gorge-feeding day prior to the fasting day. This raises the question why fasting days are implemented in zoo regimes in the first place. The observed practice of providing special enrichment on fasting days might stem from the impression that animals are not at ease when fasting after receiving a food portion basically corresponding to little more than their daily requirement on the day before, without a feeling of satiety related to gut distension. These current feeding regimes of zoo carnivores should be re-assessed. The combination of fasting days with preceding gorge-feeding, together with strenuous physical activity and cognitive challenges linked to the feeding event, might have the potential to mimic natural behaviours more closely than current practices. This should be investigated in future studies.

Introduction

In zoos, large mammalian terrestrial carnivores are conventionally fed on a daily basis (Meyer-Holzapfel 1968). Large zoo carnivores also often engage in pacing and repetitive stereotyped motor patterns (Carlstead et al. 1991; Clubb and Mason 2003; Meyer-Holzapfel 1968; Shepherdson et al. 1993), which have been linked to discrepancies between the zoo feeding regime and feeding in nature (Veasey 2017), amongst other causes. In contrast, their free-ranging counterparts neither have a fixed feeding schedule nor eat daily (Altman et al. 2005; Bosch et al. 2015). For example, Schaller (1972) reported that lions eat at an average frequency of once every 2.5 days on plains and once every 3–3.5 days in woodlands; however, hunting success rates vary a lot within seasons and habitats. In their review, De Cuyper et al. (2019) showed that kill frequency is not necessarily linked to carnivore body size, i.e. there is no consistent decrease of carnivore feeding frequency with species' body mass.

Rather, 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 year. For example, whereas several large cats and hyenas typically hunt comparatively large prey that will surpass the daily intake capacity of the predator (De Cuyper et al. 2019), similar-sized brown bears *Ursus arctos* can feed on comparatively small prey items of which they ingest a large number during a day, like salmon or berries (Rode et al. 2001; Welch et al. 1997). Whenever large carnivores subdue large prey and conditions are favourable to gorge-feed (i.e. 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

(De Cuyper et al. 2019). Thus, if they are not in a metabolic state of accruing body stores for periods of hibernation, large carnivores in natural habitats do not necessarily have to hunt every day, allowing them to be 'full and lazy' (Jeschke 2007).

To the authors' knowledge, fasting days are part of a regular schedule in large carnivore zoo husbandry for many species. Allen et al. (1996) state 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'. Data on the frequency of use of fasting days, and on specifics of their implementation, are lacking. During a larger survey on large carnivore husbandry in 44 European zoos, the peculiarities about the use of fasting days outlined in the present study were noted. These peculiarities led the authors to investigate whether husbandry guidelines recommend fasting days and describe how they should be implemented. The use of fasting days reveals how a zoo's husbandry can match or deviate from conditions encountered in natural habitats, questioning the biological background of such husbandry decisions.

Methods

Husbandry guidelines survey

Husbandry guidelines were collected from the internet, using genus and species names together with the words 'guidelines' as search terms. Guidelines that covered large carnivores were scrutinised for recommendations of fasting days and the results were documented in tabulated form.

Zoo survey

This study is part of a bigger study which was conducted with the support of the EAZA Felid TAG and Canid and Hyaenid TAG (Kleinlugtenbelt et al. 2023). Data from 44 zoos in 7 countries were collected and compiled during personal visits by CLMK; one zoo sent their information in since a personal visit was not possible due to COVID-19 restrictions. The following species were observed during feeding: tigers *Panthera tigris* (26 zoos), lions *Panthera leo* (31 zoos), jaguars *Panthera onca* (7 zoos), leopards *Panthera pardus* (15 zoos), snow leopards *Panthera uncia* (13 zoos), cheetahs *Acinonyx jubatus* (15 zoos), lynxes *Lynx lynx* (16 zoos), hyenas *Crocuta crocuta* and *Hyaena hyaena* (11 zoos), wolves *Canis lupus* (16 zoos), brown bears *Ursus arctos*, including one brown bear–polar bear hybrid (15 zoos) and polar bears *Ursus maritimus* (12 zoos). The responsible staff members were followed on their daily routines with the selected species, both from behind the scenes and from the point of view of a visitor. During personal interviews with the responsible staff members, more information about carnivore feeding regimes, schedules and methods was gained. The interview was based on a pre-planned set of questions but was conducted as a free-flowing conversation rather than a structured listing of the individual questions. All interviews were conducted by CLMK and feeding was documented with photos and videos.

Results

Husbandry guidelines

Twenty-four husbandry guidelines were found for 25 large carnivore species, with the majority of guidelines originating from recognised organisations such as the European Association of Zoos and Aquaria (EAZA) and the Association of Zoos and Aquariums and its Species Survival Plans (SSPs) (Table 1). Generally, fasting days are suggested in husbandry guidelines as part of feeding schedules for several large carnivores (all large felids, spotted hyena, grey wolf, red wolf *Canis rufus*, dhole *Cuon alpinus* and polar bear). Typically, one or two fasting days are recommended per week, and two fasting days per week are repeatedly stated as a maximum.

Some guidelines explicitly state that fasting days are not essential (cheetah: Marker and Schumann 1998; lion: Hillermann 2009), do not mention fasting days at all (American black bear *Ursus americanus*: Lubiw-Hazard 2000; maned wolf *Chrysocyon brachyurus*: SSP 2007a; polar bear: AZA Bear TAG 2009) or discourage fasting days (brown bear: Lorenzo 2009; sloth bear *Melursus ursinus* and sun bear *Helarctos malayanus*: AZA Bear TAG 2019).

Whenever suggested, fasting days are reported to be beneficial for obesity management, or as an opportunity to feed bones and/ or small whole prey for dental health, enrichment and nutritional purposes. The feeding of bones on fasting days is recommended repeatedly.

Whereas some texts imply that fasting days serve to mimic natural foraging behaviour (feast and famine), others specifically state that they do not fulfil this function. Only one (cheetah, EAZA 2018) out of 24 husbandry guidelines mentioned specific guidelines for the feeding practices preceding the fasting day, i.e. the necessity to gorge-feed before the fasting day in order to obtain positive effects on carnivore behaviour and avoid an increase in abnormal stereotypic behaviour. For dholes, an alternating feeding regime of feeding and fasting days is suggested with a corresponding increase in the amount of food on the feeding days (EAZA 2017). Other guidelines for tigers (Dierenfeld et al. 1994) and cheetahs (Marker and Schumann 1998; SSP 2009) suggest that whenever fasting days are implemented, the daily ration *on all feeding days* should be increased, to compensate for the energy intake that is lost during the fasting days.

Zoo survey

The majority of zoos used fasting days for felids, hyenas and wolves, but not for brown or polar bears (Table 2). Of those that used fasting days, many performed animal training on these days that included a food reward, especially with leopards—in 53% of the zoos keeping them. Gorge feeding prior to the fasting day was used by a minority of zoos—in 13% of those that kept lions, 8% of those that kept snow leopards, 6% of those keeping wolves and 4% keeping tigers. For all the other included species, no gorge-feeding regimes were in place in connection with fasting days. During interviews, it was sporadically mentioned that the training performed during fasting days partially served to compensate for an increased propensity to stereotype on these days.

Discussion

The results are remarkable because they appear to point out a discrepancy between husbandry recommendations and zoo management practice on the one hand, and the respective animals' natural lifestyle on the other hand. This raises the question why fasting days are used in zoo carnivore husbandry in the first place. An important limitation of this study is that the reasons behind the use of fasting days were not specifically requested, and therefore it is only possible to speculate that use of fasting days is due to tradition at the respective facilities.

For the omnivorous or insectivorous members of the Carnivora, like maned wolves, sloth bear, sun bear, black bear and brown bear, fasting days do not seem appropriate and are consequently also not part of the husbandry recommendations (Table 2). Gorging with a subsequent fasting day on fruit or insects has not been reported in the wild, and even though the hibernating bear species are known for high food intakes at the time of fat accretion for hibernation (e.g. Hilderbrand et al. 1999), this does not lead to fasting days spent only digesting. In hibernators such

Table 1. Summary of fasting day recommendations from husbandry guidelines.

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	Baker 2006
	gastrointestinal tract and avoid impaction	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
Spotted hyena *Crocuta crocuta*	One or 2 fasting days/week are useful for body weight management	Foote 2014
	On fasting days, large bones and small whole prey can be fed	
Large canids (coyote *Canis latrans*, red wolf *Canis rufus*, gray wolf *Canis lupus*, Mexican gray wolf *Canis lupus baileyi*, maned wolf *Chrysocyon brachyurus*, dhole *Cuon alpinus*, African wild dog *Lycaon pictus*)	Recommendation of 1 fasting day/week for red wolves	AZA Canid TAG 2012
	Varying feeding regimes (feast and famine) for enrichment	Laidlaw 2000
Gray wolf *Canis lupus*	One fasting day/week is useful for body weight management	EAZA 2017
Dhole *Cuon alpinus*	The more food dholes get, the more fasting days they should get	
	Feeding every other day and simultaneously increase the daily meal size	
Maned wolf *C. brachyurus*	No fasting days mentioned	SSP 2007a
Polar bear *Ursus maritimus*	No fasting days mentioned	AZA Bear TAG 2009
	Several zoos implement at least one fasting day/week	Lintzenich et al. 2006
Sun bear *Helarctos malayanus*	Fasting days are not appropriate	AZA Bear TAG 2019
Sloth bear *Melursus ursinus*	Fasting days are not appropriate	(AZA Bear TAG 2019)
Brown bear *Ursus arctos*	Fasting days are not appropriate	Lorenzo 2009
American black bear *Ursus americanus*	No fasting days mentioned	Lubiw-Hazard 2000

Table 2. Frequency of different kinds of fasting regimes at 44 European zoos.

Species	No fasting		Fasting day with training incl. food reward (no preceding gorge-feeding)		Fasting day without *any* food preceding gorge feeding			
					no		yes	
	n zoos	%	n zoos	%	n zoos	%	n zoos	%
Tiger	3	12	11	42	11	42	1	4
Lion	3	10	12	39	12	39	4	13
Jaguar	1	14	0	0	6	86	0	0
Leopard	1	7	8	53	6	40	0	0
Snow leopard	4	31	2	15	6	46	1	8
Cheetah	5	33	4	27	6	40	0	0
Lynx	5	31	3	19	8	50	0	0
Hyena	4	36	1	9	6	55	0	0
Wolf	2	13	4	25	9	56	1	6
Brown bear	13	87	0	0	2	13	0	0
Polar bear	11	92	0	0	1	8	0	0

as black, brown or polar bears, food reduction and fasting can be used to initiate hibernation, as indicated by various accounts of bear keepers as well as analysis by Krofel et al. (2017) who showed that the denning period of hibernating brown bears is negatively related to their access to food. In these species, fasting should probably not be used during times of maintenance or during pre-hibernation accretion of body stores. The same applies most likely to many small carnivores, including small felids, which are considered to hunt and eat several times per day (Bosch et al. 2015; Bradshaw 2006).

By contrast, many large felids, hyenas and canids are known to often have an alternating pattern of more active hunting, gorge-feeding days and days spent resting and digesting (see Introduction). Therefore, at first glance, the inclusion of fasting days in the husbandry management of many large carnivores might appear as an attempt to simulate conditions the animals experience in their natural habitats. On second thought, however, both the justification of the fasting days in husbandry recommendations and the actual husbandry practice speak against this interpretation.

Several husbandry guidelines state explicitly that fasting days in zoos do not reflect the gorge-fast situation in natural habitats. Rather, the main reason given for the use of fasting days is obesity control. This leads to the evident question why obesity control should be achieved by implementing fasting days rather than by an overall adjustment of the (daily) amount of diet fed. To the authors' knowledge, there is no literature on zoo carnivores supporting either concept. In human medicine, several recent reviews (most likely all covering a similar range of original studies) have concluded that intermittent fasting is no more or less efficient at reducing obesity than an equivalent diet restriction with daily food intake (Rynders et al. 2019; Stockman et al. 2018; Varady et al. 2022; Welton et al. 2020). Thus, the reason why fasting days are mentioned in husbandry guidelines appears somewhat obscure and might simply be reporting the traditional use of this measure.

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 rhythm 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 days. On the contrary, rather than focussing increased attention on the day before, it appears that with an emphasis of bone feeding (guidelines) and training with food rewards (survey) on the fasting day, both extra food and cognitive challenges are deliberately provided on this day, as if this day required a special programme. Rather than representing a day of rest after a preceding gorging and physical and cognitive exhaustion, the fasting day seems to represent a day of unrest that needs to be buffered.

Few studies have investigated the effects of fasting days; mostly, these included a gorge-feeding event prior to the fasting day, albeit without a particularly physically or cognitively challenging feeding method (Altman et al. 2005; Finch et al. 2020; Höttges et al. 2019; Lyons et al. 1997). These studies found changes in energy intake and body condition due to a change in the total amount fed per week under the new feeding regime—an effect not actually related to the fasting day, but to the weekly amount fed (Altman et al. 2005). The behavioural changes due to the gorge- fast feeding regime differed between studies, most likely due to additional details such as the time of day food was provided or animal group size and composition. In some cases, animals paced more on feeding days (feeding in the afternoon), interpreted as anticipatory pacing with animals perceiving cues that it was a feeding day (Altman et al. 2005). In other cases, animals paced more on fasting days (Höttges et al. 2019; Lyons et al. 1997). Two studies that compared a conventional and a gorge-fast feeding regime in the same animals found no change (Altman et al. 2005) or an overall decrease in pacing with the gorge-fast regime (Finch et al. 2020). In the latter case, the difference was not noticeable immediately after the diet change, but rather when assessed a second time 12 months after the change.

Höttges et al. (2019) illustrate a potential source of confusion when talking about zoo carnivore feeding regimes: in that study, animals were observed to feed during the so-called 'fasting' days—because of food items left over from previous days in their enclosure. In the case of large carcass feeding in a gorge- fast schedule, the carcass may be too large to be consumed by the animals in a single day. Höttges et al. (2019) refer to Eloff (1984) as a source for the fact that guarding a carcass, and eating repeatedly from it, can be considered a natural behaviour in the species in question, lions. If animals can still remove relevant portions of carcasses beyond only bone on the following day, this day should not be called a 'fasting' day even if no additional food is provided; this term is best reserved for days where the animals do not have the opportunity to consume food. Given that it may be logistically difficult to remove bones or skeletons from enclosures, a fasting day thus may well mean that the animals occupy themselves with those leftovers that would not be considered nutritious prey components. Such a sequence of events might additionally encourage the consumption of less digestible carcass components like skin, cartilage and bone, which may have beneficial physiological effects for carnivores (Depauw et al. 2012, 2013; Lindburg 1988).

Daily feeding of energetically adequate, yet correspondingly small amounts of food to large carnivores might never cause the distension-linked satiety feeling these animals experience in natural habitats after successfully subduing large prey (Veasey 2017). One study claimed that a gorge-fast regime with whole carcasses for gorging attained this kind of satiety (Höttges et al. 2019). They suggested that this was indicated by a clear difference in behaviour between gorging and fasting days, as opposed to no between-day differences in behaviour on a feeding regime that included one fasting day without preceding gorge feeding (Höttges et al. 2019). The relevance of filling the gut up to its limit for alternating fasting and feeding days was theoretically derived from gut capacity and prey energy estimated by De Cuyper et al. (2019); this concept can also be illustrated using the data presented by Elliott et al. (1977) for the relationship between the size of a meal and the initiation of the next search for prey in lions (Figure 1). These data indicate that a small-sized meal, as would be a typical daily large carnivore zoo ration, would not be followed by an absence of hunting activity on the next day. Feeding large carnivores such daily rations and then exposing them to a fasting day might thus even be the opposite of mimicking natural conditions.

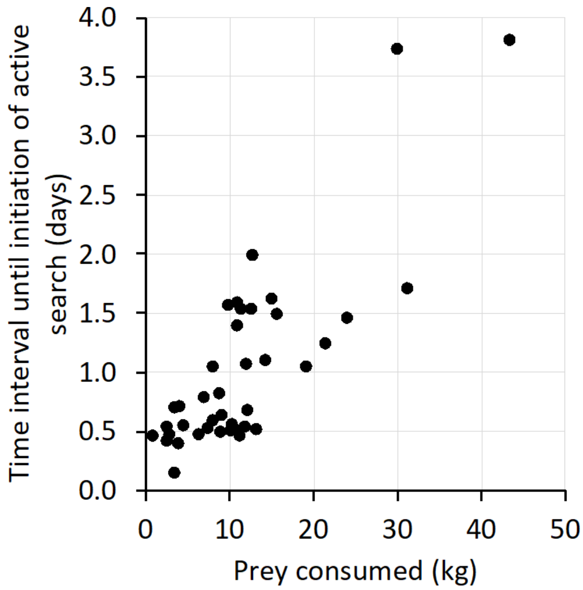

Figure 1. Relationship between the amount of prey consumed for a lion *Panthera leo* and the time until the next search for prey is initiated. Data extracted from Elliott et al. (1977) and converted from hours into days, and from calories into kg, using the given conversion factors. When consuming less 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.

Another aspect relevant to the effect of feeding on the overall behaviour and activity budget, especially on fasting days, might be the level of physical exercise and cognitive challenge linked to feeding. For example, observations that some (but not all) large felids on a gorge-fast feeding regime paced more on the feeding day after they had been fed (Lyons et al. 1997) could be considered indication that some animals might lack physical activity in relation to feeding. To the authors' knowledge, no studies evaluating the contribution of physical activity (or cognitive challenge) linked to feeding exist for zoo carnivores. The study by Krawczel et al. (2005) on circus tigers, corroborated by personal observations for another set of tigers from another circus by MC, might provide some inspiration for such investigations. These observations were not made in relation to feeding, but in relation to possibly the most exciting moment of the day for the tigers—their performance. Krawczel et al. (2005) describe increasing levels of anticipatory pacing as the moment of performance approached, and basically extreme relaxation or resting afterwards. Transferring these observations to feeding methods in zoos would mean making a gorge-feeding event physically and cognitively challenging, which might increase the difference in behaviour between feeding and fasting days. This would have to be tested in future studies. In this endeavour, 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.

In conclusion, the common practice exposing zoo carnivores to fasting days without a preceding gorge-feeding event should be re-evaluated. Developing and assessing feeding methods that combine gorge-feeding with physical and cognitive challenges may be an important next step in large carnivore husbandry.

Acknowledgements

We thank the Felid, Canid and Hyanid TAGs for their support and sincerely thank all participating zoos: Odense Zoo, Copenhagen Zoo, Randers Zoo, Scandinavian Wildlife Park, Givskud Zoo, Skærup Zoo, Borås Zoo, Orsa Predator Park, Kolmården, Parken Zoo, Skansen, Kristiansand Zoo, Rotterdam Zoo, Wildlands Adventure Zoo Emmen, Antwerpen Zoo, Zoo Planckendael, Bremerhaven Zoo, Wildlife Park Springe, Muenster Zoo, Wingst Forest Zoo, Dortmund Zoo, Krefeld Zoo, Zoom Gelsenkirchen Zoo, Cologne Zoo, Frankfurt Zoo, Neuwied Zoo, Heidelberg Zoo, Karlsruhe Zoo, Wilhelma Stuttgart, Munich Zoo, Nuremberg Zoo, Leipzig Zoo, Animal Park Berlin, Osnabrueck Zoo, Serengeti Park Hodenhagen, Hannover Zoo, Wuppertal Zoo, Schwerin Zoo, Basel Zoo, Animal Park Bern, Walter Zoo, Wildlife Park Bruderhaus, Wildlife Park Zurich Langenberg, Zurich Zoo, and their involved staff, for their time, lovely hospitality and participation in this study.

References

Alankar K.J. (2014) *Working Manual of Snow Leopard Conservation Breeding Programme.* Padmaja Naidu Himalayan Zoological Park, Darjeeling.

Allen M.E., Oftedal O.T., Baer D.J. (1996) The feeding and nutrition of carnivores. In: Kleiman D.G., Allen M.E., Thompson K.V., Lumpkin S. (eds.). *Wild Mammals in Captivity: Principles and Techniques.* Chicago, Illinois: University of Chicago Press, 139–147.

Altman J.D., Gross K.L., Lowry S.R. (2005) Nutritional and behavioral effects of gorge and fast feeding in captive lions. *Journal of Applied Animal Welfare Science* 8(1): 47–57. doi:10.1207/s15327604jaws0801_4

AZA Bear TAG (2009) *Polar Bear* (Ursus maritimus) *Care Manual*. Silver Spring, Maryland: Association of Zoos and Aquariums.

AZA Bear TAG (2019) *Sun and Sloth Bear (*Helarctos malayanus *and* Melursus ursinus*) Care Manual.* Silver Spring, Maryland: Association of Zoos and Aquariums.

AZA Canid TAG (2012) *Large Canid (Canidae) Care Manual.* Silver Spring, Maryland: Association of Zoos and Aquariums.

AZA Jaguar SSP (2016) *Jaguar (*Panthera onca*) Care Manual.* Silver Spring, Maryland: Association of Zoos and Aquariums.

AZA Lion SSP (2012) *Lion (*Panthera leo*) Care Manual.* Silver Spring, Maryland: Association of Zoos and Aquariums.

AZA Tiger SSP (2016) *Tiger (*Panthera tigris*) Care Manual.* Silver Spring, Maryland: Association of Zoos and Aquariums.

Baker R. (2006) *Husbandry Guidelines for the Tiger (*Panthera tigris*)*. Richmond, Australia: Western Institute of Sydney.

Bosch G., Hagen-Plantinga E.A., Hendriks W.H. (2015) Dietary nutrient profiles of wild wolves: Insights for optimal dog nutrition? *British Journal of Nutrition* 113(S1): S40–S54. doi:10.1017/S0007114514002311

Bradshaw J.W.S. (2006) The evolutionary basis for the feeding behavior of domestic dogs (*Canis familiaris*) and cats (*Felis catus*). *The Journal of Nutrition* 136(7): 1927S–1931S. doi:10.1093/jn/136.7.1927S

Carlstead K., Seidensticker J., Baldwin R. (1991) Environmental enrichment for zoo bears. *Zoo Biology* 10(1): 3–16. doi:10.1002/zoo.1430100103

Clubb R., Mason G. (2003) Captivity effects on wide-ranging carnivores. *Nature* 425: 473–474. doi:10.1038/425473a

De Cuyper A., Clauss M., Carbone C., Codron D., Cools A., Hesta M., Janssens G.P.J. (2019) Predator size and prey size–gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. *Oikos* 128(1): 13–22. doi:10.1111/oik.05488

Depauw S., Bosch G., Hesta M., Whitehouse-Tedd K., Hendriks W.H., Kaandorp J., Janssens G.P.J. (2012) Fermentation of animal components in strict carnivores: A comparative study with cheetah fecal inoculum. *Journal of Animal Science* 90(8): 2540–2548. doi:10.2527/jas.2011-4377

Depauw S., Hesta M., Whitehouse-Tedd K., Vanhaecke L., Verbrugghe A., Janssens G.P.J. (2013) Animal fibre: The forgotten nutrient in strict carnivores? First insights in the cheetah. *Journal of Animal Physiology and Animal Nutrition* 97(1): 146–154. doi:10.1111/j.1439-0396.2011.01252.x

Dierenfeld E., Bush M., Philips L., Montali R. (1994) Nutrition, food preparation and feeding. In: Tilson R., Brady K., Traylor-Holzer K., Armstrong D. (eds.). *Management and Conservation of Captive Tigers,* Panthera tigris. Apple Valley, Minnesota: Minnesota Zoo, 47–52.

EAZA (2004) Husbandry Guidelines Eurasian Lynx (Lynx lynx sspp.). Amsterdam, Netherlands: EAZA Executive Office.

EAZA (2017) *Best Practice Guidelines Dhole (*C. alpinus*).* Amsterdam, Netherlands: EAZA Executive Office.

EAZA (2018) *Best Practice Guidelines Cheetah (*Acinonyx jubatus*).* Amsterdam, Netherlands: EAZA Executive Office.

EAZA (2022) *Best Practice Guidelines Jaguar (*Panthera onca*).* Amsterdam, Netherlands: EAZA Executive Office.

Elliott J.P., Cowan I.M., Holling C.S. (1977) Prey capture by the African lion. *Canadian Journal of Zoology* 55(11): 1811–1828. doi:10.1139/z77-235

Eloff F.C. (1984) Food ecology of the Kalahari lion Panthera leo vernayi. Koedoe 27: 249–258. doi:10.4102/koedoe.v27i2.584

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. doi:10.19227/jzar.v8i4.475

Foote J. (2014) *Husbandry Manual for the Spotted Hyena (*Crocuta crocuta*).* Monarto, Australia: Monarto Zoo.

Hilderbrand G.V., Schwartz C.C., Robbins C.T., Jacoby M.E., Hanley T.A., Arthur S.M., Servheen C. (1999) The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77(1): 132–138. doi:10.1139/z98-195

Hillermann A. (2009) *Husbandry Guidelines for African Lion* Panthera leo. Richmond, Australia: Western Sydney Institute of TAFE.

Höttges N., Hjelm M., Hård T., Laska M. (2019) How does feeding regime affect behaviour and activity in captive African lions (*Panthera leo*)? *Journal of Zoo and Aquarium Research* 7(3): 117–125. doi:10.19227/jzar.v7i3.392

Jeschke J.M. (2007) When carnivores are “full and lazy”. *Oecologia* 152: 357–364. doi:10.1007/s00442-006-0654-2

Kleinlugtenbelt C.L.M., Burkevica A., Clauss M. (2023) Large carnivore feeding in European zoos. *Der Zoologische Garten* NF 91 (in press).

Krawczel P.D., Friend T.H., Windom A. (2005) Stereotypic behavior of circus tigers: Effects of performance. *Applied Animal Behaviour Science* 95(3–4): 189–198. doi:10.1016/j.applanim.2005.04.010

Krofel M., Špacapan M., Jerina K. (2017) Winter sleep with room service: Denning behaviour of brown bears with access to anthropogenic food. *Journal of Zoology* 302(1): 8–14. doi:10.1111/jzo.12421

Laidlaw R. (2000) Gray wolf: A Comparison of Husbandry and Housing Practices. Gravenhurst, Ontario: Zoocheck Canada Inc.

Lindburg D.G. (1988) Improving the feeding of captive felines through application of field data. *Zoo Biology* 7(3): 211–218. doi:10.1002/zoo.1430070303

Lintzenich B., Ward A., Edwards M., Griffin M., Robbins C. (2006) *Polar Bear Nutrition Guidelines*. Bozeman, Montana: Polar Bears International.

Lorenzo S. (2009) *Husbandry Manual for the Brown Bear (*Ursus arctos*).* Richmond, Australia: TAFE NSW, Richmond College.

Lubiw-Hazard N. (2000) *American Black Bear: A Comparison of Husbandry and Housing Practices*. Gravenhurst, Ontario: Zoocheck Canada Inc.

Lyons J., Young R.J., Deag J.M. (1997) The effects of physical characteristics of the environment and feeding regime on the behavior of captive felids. *Zoo Biology* 16(1): 71–83. doi:10.1002/(SICI)1098- 2361(1997)16:1<71::AID-ZOO8>3.0.CO;2-8

Marker L., Schumann B.D. (1998) Cheetahs as problem animals: Management of cheetahs on private land in Namibia (Appendix 2: Husbandry manual for cheetahs). In: Penzhorn B.L. (ed.). *Symposium on Cheetahs as Game Ranch Animals*. Onderstepoort, South Africa: Wildlife Group of the South African Veterinary Association, 90–99.

Meyer-Holzapfel M. (1968) Abnormal behavior in zoo animals. In: Fox M.W. (ed.). *Abnormal Behavior in Animals.* Philadelphia, Pennsylvania: WB Saunders, 476–503.

Rode K.D., Robbins C.T., Shipley L.A. (2001) Constraints on herbivory by grizzly bears. *Oecologia* 128: 62–71. doi:10.1007/s004420100637

Rynders C.A., Thomas E.A., Zaman A., Pan Z., Catenacci V.A., Melanson E.L. (2019) Effectiveness of intermittent fasting and time-restricted feeding compared to continuous energy restriction for weight loss. *Nutrients* 11(10): 2442. doi:10.3390/nu11102442

Shepherdson D.J., Carlstead K., Mellen J.D., Seidensticker J. (1993) The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology* 12(2): 203–216. doi:10.1002/zoo.1430120206

SSP (2000) *Clouded Leopard (*Neofelis nebulosa*) Husbandry Guidelines*. Silver Spring, Maryland: Clouded Leopard SSP Management Group.

SSP (2007a) *Maned Wolf Husbandry Manual*. Silver Spring, Maryland: Maned Wolf SSP Management Group.

SSP (2007b) *Guidelines for Captive Management of Jaguars*. Fort Worth Zoo, Texas: Jaguar SSP Management Group.

SSP (2009) *Husbandry Manual for the Cheetah (*Acinonyx jubatus*).* Silver Spring, Maryland: Cheetah SSP Management Group.

Stockman M.C., Thomas D., Burke J., Apovian C.M. (2018) Intermittent fasting: Is the wait worth the weight? *Current Obesity Reports* 7: 172–185. doi:10.1007/s13679-018-0308-9

Varady K.A., Cienfuegos S., Ezpeleta M., Gabel K. (2022) Clinical application of intermittent fasting for weight loss: Progress and future directions. *Nature Reviews Endocrinology* 18: 309–321. doi:10.1038/s41574-022- 00638-x

Veasey J.S. (2017) In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology* 36(6): 413–425. doi:10.1002/zoo.21390

Welch C.A., Keay J., Kendall K.C., Robbins C.T. (1997) Constraints on frugivory by bears. *Ecology* 78(4): 1105–1119. doi:10.1890/0012-9658(1997)078[1105:COFBB]2.0.CO;2

Welton S., Minty R., O’Driscoll T., Willms H., Poirier D., Madden S., Kelly L. (2020) Intermittent fasting and weight loss: Systematic review. *Canadian Family Physician* 66(2): 117–125.

Publication note

Body condition scores of large carnivores in 44 European zoos

Status: Revision under review

Journal: Journal of Zoo and Aquarium Research

Journal of Zoo And Aquarium Research – evidence based practice

Body condition scores of large carnivores in 44 European zoos

Cellina L. M. Kleinlugtenbelt[1], Anita Burkevica[2], Marcus Clauss[1]

[1] Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich,

Winterthurerstr. 260, 8057 Zurich, Switzerland

[2] Parken Zoo, Flackstavägen 13, 63222 Eskilstuna, Sweden

Cellina L. M. Kleinlugtenbelt: cellinaluciamaria.kleinlugtenbelt@uzh.ch 0000-0002-7073-3547
Anita Burkevica: anita.burkevica@parkenzoo.se
Marcus Clauss: mclauss@vetclinics.uzh.ch 0000-0003-3841-6207

Correspondence to: Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife,

Vetsuisse Faculty, University Zurich, Winterthurerstr 260, 8057 Zurich, Switzerland

Abstract

Zoo animals are often suspected to be prone to obesity, due to a combination of readily provided food resources and reduced opportunity for physical exercise. Here, we assessed the body condition and selected husbandry conditions (the amount of food offered, the enclosure size, or the number of enrichment measures provided) of ten large carnivore species (at 15-104 individuals per species) in 44 European zoos in seven different countries, using a standardized body condition scoring (BCS) protocol (ranging from 1-9) applied by a single investigator. In general, the BCS showed a close to normal distribution of BCS around the 'ideal' score of 5, with a slight right shift towards higher BCS; only in jaguar (*Panthera onca*) and lynx (*Lynx lynx*), BCS suggested over conditioned study populations. BCS tended towards positive correlation with body mass, except in tigers (*Panthera tigris*), leopards (*Panthera pardus*), and the two bear species (*Ursus arctos*, *U. maritimus*). Within species, the BCS was not systematically correlated to the amount of food, the enclosure size, or the number of enrichment measures. The results suggest that while both under- and overconditioned individuals exist, the study populations were largely in a body condition considered ideal. The lack of overarching correlations with simplistic husbandry proxies suggests that management of body condition occurs at the level of the individual institution with tailored measures.

Keywords: body condition score, large carnivores, enrichment, enclosure size, body mass

Introduction

Obesity is a well-known problem in zoo animals (Bray and Edwards 1999) which can be closely associated with other health issues such as reduced reproduction or reduced lifespan (Das 2018; Adji et al. 2022). Carnivores have been named among the animal groups particularly affected by obesity (Dierenfeld et al. 1994). Species may differ in terms of their intrinsic susceptibility to obesity, for example, due to a life history that includes seasonal resource fluctuations and the acquisition of body fat stores prior to hibernation. In this context, Mellor et al. (2020) found that lemur species adapted to natural feeds with a greater unpredictability of availability had a higher propensity for obesity in zoos. Among the carnivores, bears are renowned for their capacity to accrue body fat and might therefore be particularly prone to obesity in zoo settings (Lisi et al. 2013).

Obesity can in general be traced back to two main management reasons – on the one hand, evidently, an amount of energy that is too high (Lisi et al. 2013; Gerstner et al. 2016) and on the other hand, reduced incentive of spending energy via mainly physical (but potentially also, to a much lesser degree, cognitive) activity. A connection that is often made is that a small enclosure size limits the activity (Brereton 2020) and might hence contribute to a lack of energy expenditure and obesity (Lutz and Woods 2012). Additionally, there may be little incentive or motivation for activity, regardless of enclosure size. One possible reason for the latter can be a lack of so-called 'enrichment' – structural or temporal factors of animal management that provide stimuli, such as objects, materials, scents or smells that motivate and elicit a diverse repertoire of physical behaviours, stimulating and fulfilling cognitive, social and emotional needs of the animals, and inciting them to spend energy (Mellen and Sevenich MacPhee 2001; Meehan and Mench 2007; Szokalski et al. 2012; Ahloy-Dallaire et al. 2018).

In order to monitor an animal's physical condition with respect to obesity, apart from the evident management measure of regular weighing, various body condition scoring (BCS) methods are available (Schiffmann et al. 2017). The use of BCS has been proven helpful in both, gaining an overview over the current body condition status of zoo populations as well as achieving aims in management programs aimed at individual animals (Bray and Edwards 2001; Edwards et al. 2015; Clark et al. 2016; Schiffmann et al. 2019a). Typically, BCS can show correlations with body mass or a body mass index (Reppert et al. 2011; Heidegger et al. 2016; Schiffmann et al. 2019b; Clavadetscher et al. 2021), with body composition in terms of adipose tissue and muscle proportions (Morfeld et al. 2016), with the amount of food provided (Harper et al. 2001), with the amount of physical activity (Warren et al. 2011; Smit et al. 2022), and also indicate a deterioration of body condition due to health problems (Hickman and Swan 2010).

The present study was a part of a larger survey on feeding practices for large carnivores in European zoos (Kleinlugtenbelt et al. 2023a; Kleinlugtenbelt et al. 2023b). The aim of the present study was to evaluate the population BCS status in samples of several large carnivore species kept in European zoos, and to assess whether there were associations with body mass, enclosure size, the amount of food, and the applied enrichment measures.

Methods

This study was conducted with the support of the EAZA Felid TAG and Canid and Hyaenid TAG. The first author collected and compiled data from 44 zoos in seven countries by personal visits. One zoo sent their information in since a personal visit was not possible due to COVID-19 restrictions. Thus, we observed tigers (*Panthera tigris*) (26 zoos), lions (*Panthera leo*) (31 zoos), jaguars (*Panthera onca*) (7 zoos), leopards (*Panthera pardus*) (15 zoos), snow leopards (*Panthera uncia*) (13 zoos), cheetahs (*Acinonynx jubatus*) (15 zoos), lynxes (*Lynx lynx*) (16 zoos), hyenas (*Crocuta crocuta and Hyaena hyaena*) (11 zoos), brown bears (*Ursus arctos*, including one brown bear – polar bear hybrid) (15 zoos), and polar bears (*Ursus maritimus*) (12 zoos) to evaluate their body condition and record the enclosure size, and the amount of food and enrichment provided. This was done by following the responsible staff members on their daily routines with the selected species, both from behind the scenes and from the point of view of a visitor. Other results of these visits have been reported elsewhere (Kleinlugtenbelt et al. 2023a; Kleinlugtenbelt et al. 2023b).

As body condition scoring protocol, we used a 9-point scoring system following the ZIMS software (Species360, Minneapolis, MN, USA), which suggests a nine-point scale: 1 – *emaciated*, 2 – *very underconditioned*, 3 – *moderately underconditioned*, 4 – *slightly underconditioned*, 5 – *ideal*, 6 – *slightly overconditioned*, 7 – *moderately overconditioned,* 8 – *very overconditioned,* 9 – *obese*. The 'Body Condition Scoring Resource Center' of the AZA Nutrition Advisory Group was used as a starting point to find illustrated BCS schemes to guide the scoring. We used the BCS for lions from Daigle et al. (2015) for felids (Fig. A1) except for the cheetah, for which we used the dedicated BCS of Reppert et al. (2011). For bears, we used the 5-point scale of the AZA Bear TAG (2009) with intermediate stages. For canids and hyaenids, we used the BCS of Laflamme (1997). No specific training for applying BCS scores was instigated, yet, all animals were scored on site by the first author. Individuals were scored from a year on and older. Due to the logistical difficulty of acquiring good photos for the many individuals per facility within the given time frame, BCS was only applied on site and not supported or repeated using photographs.

Body mass data was either the measured weight in kg or the stated estimated weight by the responsible keeper if a scale was not available in the visited facility; notably, body mass was not estimated by the visiting author in order to avoid bias due to the impression of the body condition score. The enclosure size is the total amount of m² (as specified by the zoo) that the individual/ group is able/ allowed to use, including indoor boxes, but excluding separation boxes and enclosures which are not in use. If some enclosures are not strictly for one induvial but rather being rotated on a regular basis, the average of the enclosures were used for the evaluations.

The amount of food is given as the weekly amount per individuals in kg as fed, representing various items from meat, meat on the bone, to whole carcasses. If the amount could not be given per individual but rather for a whole group, it was divided by the number of animals living in that group, excluding new born cubs and puppies. Whenever possible, the first author weighed the amount of food provided during the visits. We decided on the weekly amount to take fasting days and different feeding schedules into consideration.

We applied an enrichment score, which is the number of different enrichment options used, having in theory no upper limit. We followed Table 1 in Hoy et al. (2010). The enrichment options were grouped into these categories but counted individually (Table A1). Olfactory enrichment was defined as addition of natural or artificial odours, scents, or the rotation of enclosures inner- and inter-species wide. Auditory and visual enrichment is included into one group and seen as the addition of sounds or visual stimuli. Tactile enrichment is the provision of novel objects, artificial, natural or parts of animals. As structural enrichment we included anything that is considered an alteration of physical space of the enclosure itself (Hoy et al. 2010). Feeding enrichment includes anything food related and edible counted as one (such as peanutbutter, fruits or vegetables etc.) and all feeding methods other than simply placing the food on the ground and hand feeding. The feeding methods are counted individually. Mixed-species enclosures are seen as social enrichment. All listed enrichment factors were counted and added to a sum without weighting of different enrichment options.

Not all information was available for all individuals. We assessed statistical correlations between the BCS (a non-continuous measure, requiring non-parametric approaches) and both body mass and the different husbandry variables with Spearman's rho. Additionally, we performed a General Linear Model (using ranked data) with BCS as the dependent variable and the enclosure size, the amount fed, and the enrichment score as the independent variables. All analyses were performed separately for each species (group), using R (R Core Team 2020). The significance level was set at 0.05, and values between 0.05 and 0.10 are referred to as trends.

Results

For most carnivore species in this study, the surveyed individuals show a close to normal distribution of BCS around the 'ideal' score of 5 (Table 1); generally, the distribution tends to be slightly shifted to the right, i.e., towards obesity, in most species (Fig. 1). The main exceptions are jaguars and lynx, with populations tending towards higher BCS overall, and the leopard with an unusual frequency of below- and above-mid value BCS.

Positive correlations between the (estimated or actually weighed) body mass and the BCS were evident in all species except tigers, lions, and the two bear species (Fig. 2, Table 2).

The enclosure size varied between zoos and was highest in bears and lowest in jaguars (Table 1). Enclosure size was generally not correlated with BCS, except – against the expectation in a positive way – in jaguar and leopard, and in the expected, negative way in snow leopards (Table 2).

The amount fed varied between 8 and 25 kg per week and generally reflected the body size of the respective species (Table 1). Again, in most species there was no correlation with BCS, except for a positive one in lions and snow leopards, and a trend for a negative one in tigers (Table 2).

Enrichment scores varied between 0 and 24, and were particularly low in cheetahs, and particularly high in tigers (Table 1). The enrichment score also did not show a correlation with BCS in most species, expect for an unexpected, positive one in lions and leopards (Table 2).

In the General Linear Model relating to BCS, no clear picture emerged: enclosure size was mainly not significant, except for an unexpected positive association with BCS in jaguars and leopards; the amount fed had, as expected, a positive association in lions and lynx but an unexpected, negative one in tigers, and the enrichment score never showed the expected negative association, but unexpected positive ones in tigers, leopards, and cheetahs (Table 2).

Discussion

The distribution of the BCS in our survey suggest that for most species, no particular indication for widespread obesity exists. If one considered the 44 zoos visited in the present study representative for the European population, this would translate into the finding that obesity needs not be assumed as the general state of large carnivore zoo populations. Evidently, this does not mean that attention to individual animals can be relaxed – it is rather a statement of relevance for a general state of carnivore husbandry. In nearly every species, individual animals with an obese body condition were found, which all represent cases that require, in theory, management adjustments. Because, to our knowledge, no similar surveys exist for carnivores or individual species, there is no basis for detecting a temporal trend in carnivore husbandry in this respect.

Various limitations apply to the present survey. Body condition scores were not corroborated by several independent scorers, and were not documented photographically. Body mass estimates were used that may vary distinctively in terms of accuracy. Various different ways of representing enclosure size (e.g., accounting for non-accessible spaces or spaces of limited use) or of quantifying enrichment could have been used. Ideally, rather than just recording the average amount of food provided, detailed recording of actual intakes and the nutrient composition of the provided food would have been desirable. While we consider it unlikely that any of these measures, which were beyond the logistical and financial scope of the present study, would have changed the results in a systematic way, we cannot claim this with confidence. However, we emphasize that these limitations may well reflect those of zoos actually applying the same monitoring process. With respect to highly seasonal species – in the context of the present study, the bears – a single time point-assessment of body condition cannot be considered adequate, but a documentation of the seasonal course of body condition would be required.

Under ideal, controlled conditions, we would expect a correlation of the BCS with the body mass of the individuals of a species. Such a correlation should be more distinct in species with a restricted size range and be weaker to non-existent in species where adult individuals can have a broad body size range. In the present study, the finding that for many species, the BCS-body mass correlation was significant or tended towards significance, with the exception of the tiger and the bears, supports this concept. The main exception was the leopard, in which the visual impression of a correlation (Fig. 2D) was not corroborated statistically (Table 2). Generally, but most particularly in species with a wide body mass range for mature individuals, the BCS is better compared to a body mass index, where the body mass is compared to the actual size of the animal (Labocha et al. 2014). This is because we do not expect large individuals to have a higher BCS, but individuals that are heavy for their respective size. For the present study, establishing a body mass index for the carnivores was not feasible. The general agreement with body mass (estimates) found in the present survey simply corroborates the often-repeated observation that BCS is a useful tool for monitoring. Body condition monitoring, either by weighing or by (photography-supported) BCS, should be part of any modern animal husbandry system.

Surveys such as the present one do not follow an experimental setup, in which cause and effect can be clearly separated. Zoo animal management is a process of constant adjustment, and hence correlations of management determinants with BCS can theoretically yield any outcome, all of which can be conveniently interpreted: if BCS correlates positively with the amount of food provided, for example, this can be interpreted as a simple cause-effect where the majority of the surveyed population is on the feeding regime that triggers these BCS. If BCS correlates negatively with the amount of food provided, this can be interpreted as a population-wide reaction of managers to reduce the amount of food in individuals that appear obese, and to increase the amount of food in individuals that appear too thin. Any absence of a relationship between the BCS and the provided food can be interpreted as a mix of both scenarios across the respective population. The same logic applies to the enrichment provided, which might be the cause or a reaction to a specific condition.

Regardless of the findings of a survey such as ours, there can be no doubt that the amount of food provided, and the amount of physical exercise actually done by an animal, will have effects on its body condition (Heuberger and Wakshlag 2011; Morrison et al. 2013). Treatment of obesity is typically done by reducing the caloric intake, either by reducing the amount fed, reducing the energy density in the food provided, or both. In carnivores, providing whole prey as compared to meat-only diets could represent such a reduction in energy density, and, due to the effects of more difficult-to-digest parts of whole prey that are subject to bacterial degradation in the hindgut, nevertheless trigger a feeling of satiety (e.g. as suggested in Depauw et al. 2013). By contrast, increasing exercise typically has a less distinct effect on body condition than caloric restriction. In companion animals in which exercise can be easily increased intentionally, such as dogs and horses, exercise appears a more promising weight control approach (Butterwick and Hawthorne 1998; German 2006; Moore et al. 2019) than in animals where the incentives for movement can only be given indirectly. This does not mean that exercise-enhancing enrichment should not be given – it is, on the contrary, one of the hallmarks of professional animal husbandry aimed at providing for many aspects of welfare. But one should not consider it as a major component of a weight management program.

In our survey, both enclosure size and enrichment were considered as potential factors linked to physical exercise. The overall lack of evident correlations with BCS bespeak the well-known fact that while both factors are important components of welfare, they cannot be equated with the amount of exercise and energy expenditure. Whether an enclosure will trigger activity of its inhabitants will depend on additional factors, such as the specific placement of points of interest (location of feeding, drinking, comfort, exploration) and the provision of enrichment that makes different locations attractive (Powell 1995). The availability of space does not automatically raise an individual’s activity level (Galardi et al. 2021), even though Breton and Barrot (2014) described a positive correlation between the size of the enclosure and the total daily distance covered by tigers. These aspects cannot be covered in the simple square metre measurements and enrichment counts used in the present study. Consequently, we repeat the well-known fact that the efficacy of enclosures and enrichment needs to be assessed on a case-by-case basis. As a side note, one peculiar finding of the present survey were the large enclosure areas provided to bear species (Table 1). This corresponds to a trend described previously where traditionally small bear enclosures have been replaced increasingly by large enclosures (Kawata 2012). The focus on bears, in this respect, appears mainly triggered by their historically particularly restricted conditions; the appropriateness of similarly large enclosures for other carnivores is out of the question.

Conclusion

In conclusion, the large carnivore population surveyed in the present study generally showed a ‘normal’ body condition with only very slight tendencies towards obesity. Body condition corresponded to body mass data in several species, as one would expect. There were no systematic relationships between body condition and enclosure size, amount of food offered, or the amount of enrichment provided. In other words, no broad-brush statements can be made as explanations for high or low body condition. Rather, body condition management occurs at the level of the individual facility, where a set of specific measures has a collective effect on the animal.

Acknowledgements

We thank the Felid, Canid and Hyaenid TAGs for their support and sincerely thank all participating Zoos (Belgium: Antwerpen Zoo, Zoo Planckendael; Denmark: Givskud Zoo Zootopia, København Zoo, Odense Zoo, Randers Regnskov, Scandinavisk Dyrepark, Skærup Zoo; Germany: Allwetterzoo Münster, Der Grüne Zoo Wuppertal, Erlebnis-Zoo Hannover, Kölner Zoo, Serengeti Park Hodenhagen, Tiergarten Nürnberg, Tierpark Berlin, Tierpark Hellabrunn, Wingster Waldzoo, Wilhelma Stuttgart, Wisentgehege Springe, Zoo am Meer Bremerhaven, Zoo Dortmund, Zoom Erlebniswelten, Zoo Frankfurt, Zoo Heidelberg, Zoo Krefeld GmbH, Zoo Leipzig, Zoologischer Stadtgarten Karlsruhe, Zoologischer Garten Schwerin, Zoo Neuwied, Zoo Osnabrück; Netherlands: Diergaarde Blijdorp, Wildlands Adventure Zoo Emmen; Norway: Dyreparken Kristiansand; Sweden: Borås Djurpark, Kolmården, Orsa Rovdjurpark, Parken Zoo, Skansen; Switzerland: Tierpark Bern, Walter Zoo, Wildnispark Zürich Langenberg, Wildpark Bruderhaus Winterthur, Zoo Basel, Zoo Zürich) and their involved staff, for their time, hospitality and participation in this study. We thank Christian Schiffmann and an anonymous reviewer for constructive comments that improved the manuscript.

References

Adji AV, Pedersen AØ, Agyekum AK (2022) Obesity in pet rabbits: A narrative review. Journal of Exotic Pet Medicine 41: 30-37

Ahloy-Dallaire J, Espinosa J, Mason G (2018) Play and optimal welfare: Does play indicate the presence of positive affective states? Behavioural Processes 156: 3-15

AZA Bear TAG (2009) Polar bear (*Ursus maritimus*) care manual. Association of Zoos and Aquariums, Silver Spring, MD

Bray RE, Edwards MS (1999) Body condition scoring of captive (zoo) equids. Proceedings of the AZA Nutrition Advisory Group Conference Columbus, OH: AZA Nutrition Advisory Group 3:

Bray RE, Edwards MS (2001) Application of existing domestic animal condition scoring systems for captive zoo animals. Proceedings of the Conference of the Nutrition Advisory Group 4: 25-28

Brereton JE (2020) Directions in animal enclosure use studies. Journal of Zoo and Aquarium Research 8: 1-9

Breton G, Barrot S (2014) Influence of enclosure size on the distances covered and paced by captive tigers (*Panthera tigris*). Applied Animal Behaviour Science 154: 66-75

Butterwick RF, Hawthorne AJ (1998) Advances in dietary management of obesity in dogs and cats. Journal of Nutrition 128: 2771S-2775S

Clark A, Silva-Fletcher A, Fox M, Kreuzer M, Clauss M (2016) Survey of feeding practices, body condition and faeces consistency in captive ant-eating mammals in the UK. Journal of Zoo and Aquarium Research 4: 183-195

Clavadetscher I, Bond ML, Martin LF, Schiffmann C, Hatt J-M, Clauss M (2021) Development of an image-based body condition score for giraffes (*Giraffa camelopardalis*) and a comparison of zoo-housed and free-ranging individuals. Journal of Zoo and Aquarium Research 9: 170-185

Daigle CL, Brown JL, Carlstead K, Pukazhenthi B, Freeman EW, Snider RJ (2015) Multi-institutional survey of social, management, husbandry and environmental factors for the SSP A frican lion *Panthera leo* population: examining the effects of a breeding moratorium in relation to reproductive success. International Zoo Yearbook 49: 198-213

Das A (2018) Current trends in feeding and nutrition of zoo animals: A review. Indian Journal of Animal Nutrition 35: 242-250

Depauw S, Hesta M, Whitehouse-Tedd K, Vanhaecke L, Verbrugghe A, Janssens GPJ (2013) Animal fibre: The forgotten nutrient in strict carnivores? First insights in the cheetah. Journal of Animal Physiology and Animal Nutrition 97: 146-154

Dierenfeld E, Bush M, Phillips L, Montali R (1994) Nutrition, food preparation and feeding. In: Tilson R, Brady K, Traylor-Holzer K, Armstrong D (eds) Management and conservation of captive tigers, *Panthera tigris*. Minnesota Zoo, Apple Valley, Minnesota, pp 47-52

Edwards KL, Shultz S, Pilgrim M, Walker SL (2015) Irregular ovarian activity, body condition and behavioural differences are associated with reproductive success in female eastern black rhinoceros (*Diceros bicornis michaeli*). General and Comparative Endocrinology 214: 186-194

Galardi EG, Fabbroni M, Rausa FA, Preziosi R, Brereton JE, Pastorino GQ (2021) An investigation into the behavior, sociality and enclosure use of group-housed lions and tigers. Journal of Veterinary Medicine and Animal Science 4: 1068

German AJ (2006) The growing problem of obesity in dogs and cats. Journal of Nutrition 136: 1940S-1946S

Gerstner G, Liesegang A, Hatt J-M, Clauss M, Galeffi C (2016) Seasonal body mass changes and feed intake in spectacled bears (*Tremarctor ornatus*) at Zurich Zoo. Journal of Zoo and Aquarium Research 4: 121-126
Harper EJ, Stack DM, Watson TDG, Moxham G (2001) Effects of feeding regimens on bodyweight, composition and condition score in cats following ovariohysterectomy. Journal of Small Animal Practice 42: 433-438
Heidegger E, von Houwald F, Steck B, Clauss M (2016) Body condition scoring system for greater one-horned rhino (*Rhinoceros unicornis*): development and application. Zoo Biology 35: 432-443
Heuberger R, Wakshlag J (2011) The relationship of feeding patterns and obesity in dogs. Journal of Animal Physiology and Animal Nutrition 95: 98-105
Hickman DL, Swan M (2010) Use of a body condition score technique to assess health status in a rat model of polycystic kidney disease. Journal of the American Association for Laboratory Animal Science 49: 155-159
Hoy JM, Murray PJ, Tribe A (2010) Thirty years later: Enrichment practices for captive mammals. Zoo Biology 29: 303-316
Kawata K (2012) Exorcising of a cage: a review of American zoo exhibits, part iii. Zoologische Garten NF 81: 132-146
Kleinlugtenbelt CLM, Burkevica A, Clauss M (2023a) Large carnivore feeding in European zoos. Der Zoologische Garten NF 91: (in press)
Kleinlugtenbelt CLM, Clauss M, Burkevica A, De Cuyper A (2023b) Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry. Journal of Zoo and Aquarium Research (in press):
Labocha MK, Schutz H, Hayes JP (2014) Which body condition index is best? Oikos 123: 111-119
Laflamme D (1997) Development and validation of a body condition score system for dogs. Canine Practice 22: 10-15
Lisi KJ, Barnes TL, Edwards MS (2013) Bear weight management: a diet reduction plan for an obese spectacled bear (*Tremarctos ornatus*). Journal of Zoo and Aquarium Research 1: 81-84
Lutz TA, Woods SC (2012) Overview of animal models of obesity. Current Protocols in Pharmacology 58: 5.61.61-65.61.18
Meehan CL, Mench JA (2007) The challenge of challenge: can problem solving opportunities enhance animal welfare? Applied Animal Behaviour Science 102: 246-261
Mellen J, Sevenich MacPhee M (2001) Philosophy of environmental enrichment: past, present, and future. Zoo Biology 20: 211-226
Mellor EL, Cuthill IC, Schwitzer C, Mason GJ, Mendl M (2020) Large lemurs: ecological, demographic and environmental risk factors for weight gain in captivity. Animals 10: 1443
Moore JL, Siciliano PD, Pratt-Phillips SE (2019) Effects of diet versus exercise on morphometric measurements, blood hormone concentrations, and oral sugar test response in obese horses. Journal of Equine Veterinary Science 78: 38-45
Morfeld KA, Meehan CL, Hogan JN, Brown JL (2016) Assessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American Zoos and management practices associated with high body condition scores. PLoS One 11: e0155146
Morrison R, Penpraze V, Beber A, Reilly JJ, Yam PS (2013) Associations between obesity and physical activity in dogs: a preliminary investigation. Journal of Small Animal Practice 54: 570-574

Powell DM (1995) Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*). Animal Welfare 4: 361-370

R Core Team (2020) R: A language and environment for statistical computing. version 3.6.3. R Foundation for Statistical Computing, Vienna, http://www.R-project.org/. In:

Reppert A, Treiber K, Ward A (2011) Body condition scoring in cheetah (*Acinonyx jubatus*) advancements in methodology and visual tools for assessment. Proceedings of the Ninth Conference on Zoo and Wildlife Nutrition, AZA Nutrition Advisory Group, Kansas City, MO:

Schiffmann C, Clauss M, Hoby S, Hatt J-M (2017) Visual body condition scoring in zoo animals – composite, algorithm and overview approaches in captive Asian and African elephants. Journal of Zoo and Aquarium Research 5: 1-10

Schiffmann C, Clauss M, Hoby S, Codron D, Hatt J-M (2019a) Body Condition Scores (BCS) in European zoo elephants' (*Loxodonta africana* and *Elephas maximus*) lifetimes – a longitudinal analysis. Journal of Zoo and Aquarium Research 7: 74-86

Schiffmann C, Clauss M, Hoby S, Hatt J-M (2019b) Weigh and see – body mass recordings versus body condition scoring (BCS) in zoo elephants (*Loxodonta africana* and *Elephas maximus*). Zoo Biology 39: 97-108

Smit M, Corner-Thomas RA, Weidgraaf K, Thomas DG (2022) Association of age and body condition with physical activity of domestic cats (*Felis catus*). Applied Animal Behaviour Science 248: 105584

Szokalski MS, Litchfield CA, Foster WK (2012) Enrichment for captive tigers (*Panthera tigris*): Current knowledge and future directions. Applied Animal Behaviour Science 139: 1-9

Warren BS, Wakshlag JJ, Maley M, Farrell TJ, Struble AM, Panasevich MR, Wells MT (2011) Use of pedometers to measure the relationship of dog walking to body condition score in obese and non-obese dogs. British Journal of Nutrition 106: S85-S89

Table 1 Descriptive statistics of the large carnivores scored for their body condition (BCS ranging from 1-9) and the enclosure size, the amount of fresh food fed per week, and the enrichment score of the enclosure.

Species (n)	**BCS median [min-max] (mean ±SD)**	**Enclosure size m²**	**Amount fed mean ±SD [min-max] kg as fed/week**	**Enrichment score n**
Tiger (66)	5 [3-9] (5.2 ±1.1)	1840 ±2464 [15-10000]	25 ±11 [10-50]	13 ±5 [4-21]
Lion (104)	5 [3-9] (5.4 ±1.1)	5321 ±8826 [150-40000]	20 ±7 [10-35]	9 ±3 [3-17]
Jaguar (15)	6 [3-8] (5.9 ±1.5)	510 ±258 [135-900]	16 ±7 [7-30]	8 ±3 [5-11]
Leopard (26)	5 [2-7] (5.0 ±1.3)	671 ±1004 [40-3400]	11 ±3 [6-17]	10 ±4 [3-18]
Snow leopard (26)	5 [4-8] (5.7 ±0.9)	1082 ±1459 [40-5400]	13 ±4 [8-26]	10 ±5 [3-18]
Cheetah (47)	5 [3-7] (5.2 ±0.9)	2316 ±1981 [200-6700]	9 ±4 [5-21]	6 ±4 [0-17]
Lynx (20)	6 [4-8] (5.8 ±1.2)	1792 ±1341 [80-550]	8 ±3 [4-13]	7 ±4 [1-14]
Hyena (24)	5 [3-8] (5.1 ±0.9)	1209 ±965 [250-2850]	9 ±3 [4-12]	8 ±4 [1-17]
Brown bear (47)	5 [4-7] (5.0 ±0.6)	10709 ±8131 [413-25000]	30 ±15 [20-60]	5 ±8 [1-11]
Polar bear (32)	5 [4-7] (5.1 ±0.8)	5383 ±10263 [540-33400]	30 ±15 [20-60]	5 ±8 [1-11]

Table 2 Nonparametric correlations (using Spearman's correlation coefficient rho and the p-value) of the body condition score (BCS) with individual characteristics of the animals (right side of table) and results of a General Linear Model (GLM; based on ranked data; using the t-statistic and the p-value) assessing the relationship of BCS with enclosure size, the amount of food, and the enrichment score. Significant results set in **bold**, and trends set in *italics*.

Species	**Correlations with BCS**				**GLM**		
	Body mass	**Enclosure size**	**Amount fed**	**Enrichment score**	**Enclosure size**	**Amount fed**	**Enrichment score**
			rho **p**			**t** **p**	
Tiger	-0.02	0.03	*-0.22*	**0.27**	0.64	**-2.50**	**2.46**
	0.872	0.809	*0.075*	**0.029**	0.525	**0.015**	**0.017**
Lion	*0.21*	-0.15	**0.20**	0.04	-0.73	**2.40**	-0.31
	0.092	0.140	**0.042**	0.673	0.465	**0.018**	0.755
Jaguar	**0.89**	**0.58**	*0.49*	-0.07	**2.71**	0.84	-0.75
	0.001	**0.025**	*0.092*	0.818	**0.024**	0.423	0.473
Leopard	0.27	**0.41**	-0.07	0.08	**3.11**	0.68	**2.13**
	0.229	**0.040**	0.730	0.702	**0.005**	0.502	**0.044**
Snow leopard	**0.49**	**-0.47**	**0.39**	0.29	-1.38	1.24	0.78
	0.048	**0.016**	**0.047**	0.155	0.182	0.229	0.442
Cheetah	**0.45**	0.06	-0.11	**0.32**	050	0.50	**2.70**
	0.003	0.695	0.469	**0.027**	0.623	0.618	**0.010**
Lynx	*0.95*	-0.24	0.26	0.03	-0.72	*1.89*	1.43
	0.051	0.301	0.307	0.908	0.485	*0.079*	0.176
Hyena	*0.60*	0.24	0.20	0.10	0.79	0.46	0.45
	0.088	0.280	0.338	0.657	0.440	0.648	0.659
Brown bear	-0.01	0.09	-	0.08	0.56	-	0.70
	0.953	0.646		0.588	0.578		0.486
Polar bear	**-0.55**	*-0.31*	-	0.07	-1.35	-	-0.34
	0.016	*0.091*		0.703	0.189		0.735

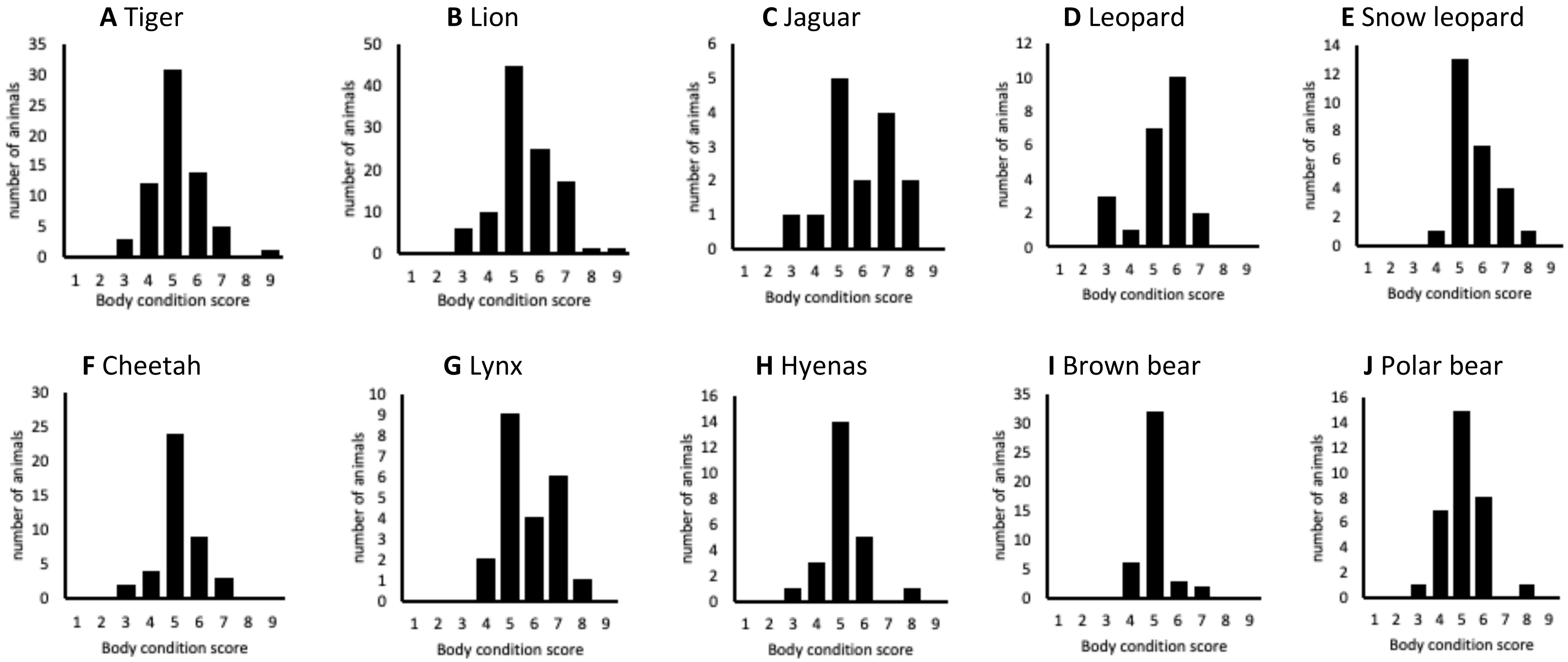

Figure 1. Body condition score distribution in 10 different large carnivores across 44 European zoos.

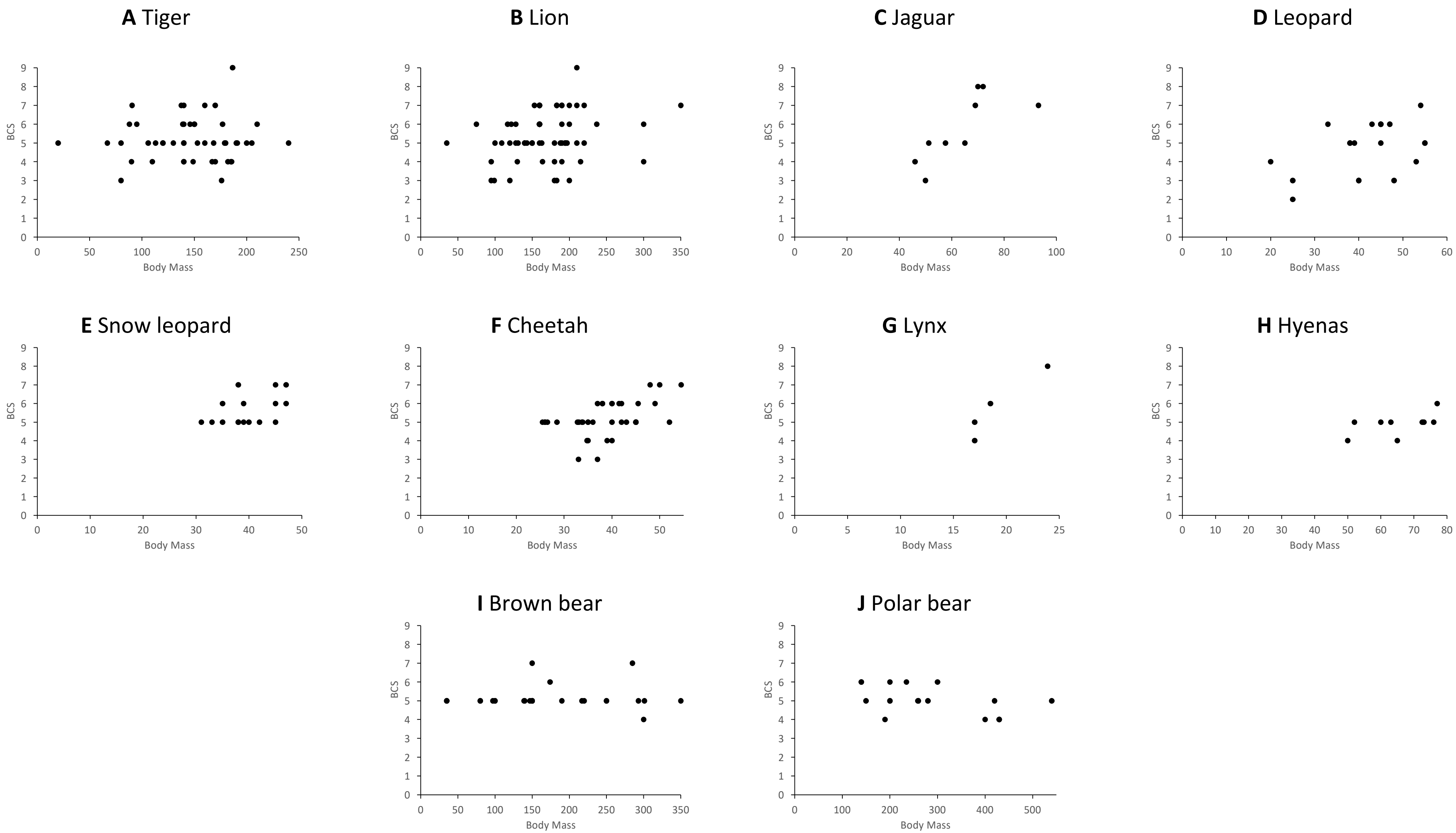

Figure 2. Body condition score in relation to the body mass (kg) in 10 different large carnivores.

Appendix

Table A1 Different enrichment categories and options provided by the 44 included institutions throughout all species (following Hoy et al. 2010).

olfactory enrichment	auditory/ visual enrichment	tactile enrichment	structural enrichment	social enrichment	feeding enrichment
enclosure rotations (within species)	view to other enclosures	tires / barrels	brushes	interspecies enclosures	Feeding methods*
enclosure rotation (between species)		ropes / fire hose	ground substance change (sand, leaves, woodchips)		Food related goods
rotation of toys or enclosure interior between species		swings	complete enclosure redesign		
wool/fur/skin/ feather		balls	pile of leaves		
blood trail		blankets/ towels	branches/ logs/trees		
faeces/ bedding between species		paper pipes (filled or empty)			
scents/ smells		cartons/ bags/ baskets (filled or empty)			
		hanging object			
		furniture			
		kid toys (plastic)			
		swimming object			
		horns/ antlers			
		horsetails			
		hoof/claws			
		artificial/real honeycomb other self-built options			

*detailed in Kleinlugtenbelt et al. (2023a)

SCORE	DESCRIPTION
1	Ribs visible; no palpable fat; severe abdominal tuck; lumbar vertebrae and wings of ilea easily palpated
2	Ribs easily visible; lumbar vertebrae obvious with minimal muscle mass; pronounced abdominal tuck; no palpable fat
3	Ribs easily palpable with minimal fat covering; lumbar vertebrae obvious; obvious waist behind ribs; minimal abdominal fat
4	Ribs palpable with minimal fat covering; noticeable waist behind ribs; slight abdominal tuck; abdominal fat pad present
5	Well-proportioned; observe waist behind ribs; ribs palpable with slight fat covering; abdominal fat pad minimal
6	Ribs palpable with slight excess fat covering; waist and abdominal fat pad distinguishable but not obvious; abdominal tuck absent
7	Ribs not easily palpated with moderate fat covering; waist poorly discernible; obvious rounding of abdomen; moderate abdominal fat pad
8	Ribs not palpable with excess fat covering; waist absent; obvious rounding of abdomen with prominent abdominal fat pad; fat deposits present over lumbar area
9	Ribs not palpable under heavy fat cover, heavy fat deposits over lumbar area, face and limbs; distention of abdomen with no waist; extensive abdominal fat deposits

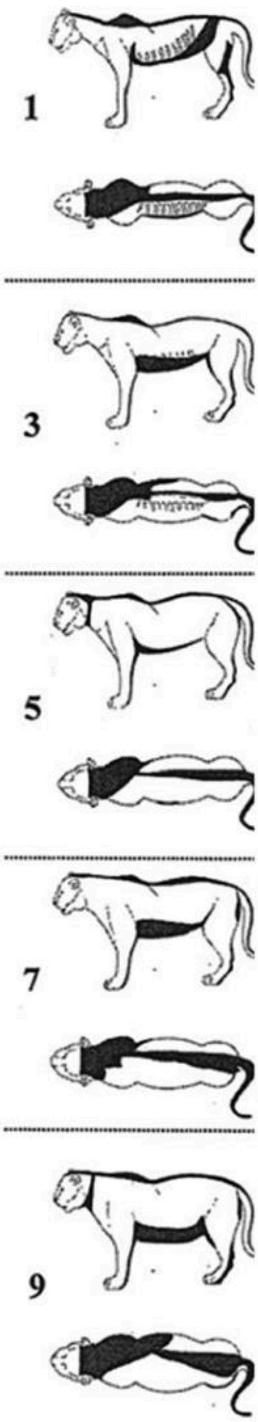

Figure A1 Example of a BCS scheme for lions from Daigle et al. (2015).

Acknowledgement

I would like to express my appreciation to all people who contributed in some way to the work described in this thesis. First and foremost, I thank my supervisor Prof. Dr. vet. med. Marcus Clauss, for his continuous support on my study and research, his invaluable enthusiasm, knowledge, motivation, and guidance that helped me write and finalize this thesis. I could not have imagined a better supervisor for my thesis.
Furthermore, I am extremely grateful to Anita Burkevica who always supported me and being not only a Co-Author but also a mentor and without who I would not be able to already be gotten closer to my dreams and goals in the zoo world. Thanks to her help we were also able to get in contact with the zoos on the Scandinavian site.

Special thanks of course to all participating zoos (Belgium: Antwerpen Zoo, Zoo Planckendael; Denmark: Givskud Zoo Zootopia, København Zoo, Odense Zoo, Randers Regnskov, Scandinavisk Dyrepark, Skærup Zoo; Germany: Allwetterzoo Münster, Der Grüne Zoo Wuppertal, Erlebnis-Zoo Hannover, Kölner Zoo, Serengeti Park Hodenhagen, Tiergarten Nürnberg, Tierpark Berlin, Tierpark Hellabrunn, Wingster Waldzoo, Wilhelma Stuttgart, Wisentgehege Springe, Zoo am Meer Bremerhaven, Zoo Dortmund, Zoom Erlebniswelten, Zoo Frankfurt, Zoo Heidelberg, Zoo Krefeld GmbH, Zoo Leipzig, Zoologischer Stadtgarten Karlsruhe, Zoologischer Garten Schwerin, Zoo Neuwied, Zoo Osnabrück; Netherlands: Diergaarde Blijdorp, Wildlands Adventure Zoo Emmen; Norway: Dyreparken Kristiansand; Sweden: Borås Djurpark, Kolmården, Orsa Rovdjurpark, Parken Zoo, Skansen; Switzerland: Tierpark Bern, Walter Zoo, Wildnispark Zürich Langenberg, Wildpark Bruderhaus Winterthur, Zoo Basel, Zoo Zürich) and their responsible staff members who made it possible to collect all the data for our study and were more than welcome and helpful towards me during the visits.

Thanks should also go to the Felid TAG Dr. Alexander Sliwa and the Canid & Hyaenid TAG Simon Marsh for their support in our study and my Co-Author Annelies De Cuyper for her time and support in one of our papers.

Finally, I would like to give a huge thank you to my family for supporting me and believing in my goals.

Curriculum Vitae

Name, Surname	Cellina Lucia Maria Kleinlugtenbelt
Date of birth	01.08.1996
Place of birth	Baden-Baden, Germany
Nationality	German/Dutch
	Gymnasium
09/2008 – 05/2014	Pädagogium Baden-Baden, Baden-Baden, Germany
06/2011 – 12/2011	Citiepoint Christian College, Brisbane, Australia
30/05/2014	**Abitur**
	Studies of Veterinary Medicine
09/2015 – 09/2016	Szent István University, Budapest, Hungary
09/2016 – 03/2021	Tiermedizinische Hochschule Hannover, Germany
29/03/2021	**Veterinary Medicine Degree examination**
06/2021 – 09/2021	**Junior veterinarian for Zoo Animals** Parken Zoo, Eskiltuna, Sweden
07/2021 – 04/2023	**Preparation of the thesis** Under the direction of Prof. Dr. med. vet. Marcus Clauss at the Department for Small Animals, Clinic for Zoo Animals, Exotic Pets and Wildlife of the Vetsuisse Faculty University of Zurich Director: Prof. Dr. med. vet. Jean-Michel Hatt
	Veterinary Intern
02/2022 – 08/2022	Evidensia Tierärztliche Klinik für Kleintiere Norderstedt GmbH, Norderstedt, Germany