

Large carnivore feeding in European zoos

Die Fütterung großer Carnivoren in europäischen Zoos

Cellina L.M. Kleinlugtenbelt¹, Anita Burkevica² & Marcus Clauss¹

¹Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland

²Parken Zoo, Flackstavägen 13, 63222 Eskilstuna, Sweden

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 accompanying 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 institutions reported a certain repertoire of feeding methods of varying potential enrichment value, during the visits themselves, most institutions used those methods of their feeding repertoire that can be considered less labour-intensive and less enriching. The number of institutions that only used a limited number of feeding methods was unexpectedly high, and methods like swing pole feeders, pulley feeders or self-serving feeders (excl. time-delayed feeders and barrel feeders in bears) were not in use in the visited institutions. 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 facilities, equipment, diet items, and work time are available.

Keywords: carnivores, feeding methods, feeding enrichment, pole feeding, whole carcass, animal fibre

*Corresp. author:

E-Mail: mclauss@vetclinics.uzh.ch (Marcus Clauss)

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 criticised in terms of behavioural deficits (Clubb & 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 & Lindburg, 1990; Roe & 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 summarised as ‘animal fibre’, i.e., bones, tendons, cartilage, skin, hair, and feathers including collagens, glycosaminoglycans and keratin (Depauw et al., 2012, 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, 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, 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 foraging 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 & Lemon (2001) found that a pack of African wild dogs (*Lycaon pictus*) 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 (*Acinonyx jubatus*), Bond & 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; Höttinges et al., 2019). Therefore, the use of whole prey feeding has been advocated from a behavioural point of view. Table 1 gives an overview of typical diet items used in carnivore feeding.

Similarly, different ways exist that make obtaining food a more complex procedure. Evidently, a lump of minced meat put in front of the animal requires less time for ingestion than the same quantity 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 quantities 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, but less feasible for animals feeding on larger prey. For animals of the latter group, a variety of methods have been proposed to make access to diet items more

Tab. 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 but without bones – mainly from large (prey*) animals	23%	10%
Carcass parts with fur/feathers	Carcass parts with meat attached to bone, skin and fur (e.g., ¼ deer carcass cut up) – mainly from large (prey*) animals	57%	12%
½ carcass	½ carcass with skin and fur intact and 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

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).

Tab. 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 & Ha, 2014)	68%	47%
Hiding	Hiding the food within the enclosure	(Fischbacher & 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 & Schmid, 1999)	9%	25%

NA not assessed in the present study

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 in the devils' enclosure and left dangling above the ground. This should increase the 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 to 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 jumping 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 vary 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 zoological institutions have successfully been using several poles for the corresponding

Tab. 3: 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 & 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 hole 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 & Ha, 2014)	0%	0%
Movement dispenser	Object with holes, comes in all different shapes, and sizes which releases food when moved around	(Law & Kitchener, 2002; Law & Reid, 2010; Hare & 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	Zipline 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 & 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%

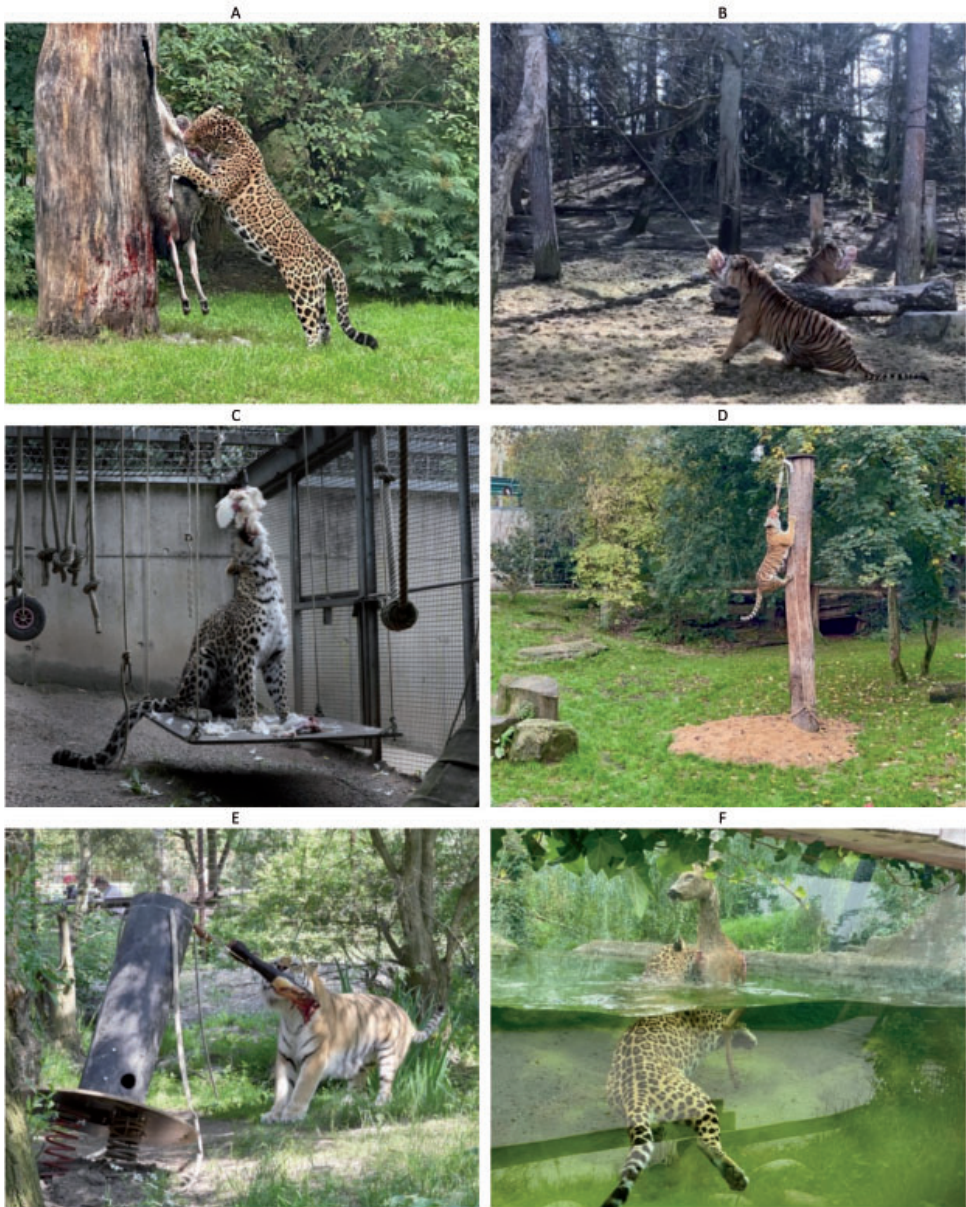


Fig. 1: Examples of different feeding methods for large carnivores: (A) carcass tied to a tree, Parken Zoo, Sweden; (B) counter-pulling system for two animals, Parken Zoo, Sweden; (C) swinging platform – Cologne Zoo, Germany; (D) pole feeding, Cologne Zoo, Germany; (E) self-built feeding object, Odense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

number of animals simultaneously. The carnivore climbs 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 deer (*Rusa unicolor*) (Turner & 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 & 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 & Jones, 2018) (Fig. 1C).

A specialised coursing system often called the ‘cheetah run’ has been adopted at various institutions worldwide to simulate the cheetah’s hunting 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 sometimes 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 (Hare & Jones, 2018). Ideally set on a hillside enclosure the food item 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 & Jones, 2018) (Fig. 2A). 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 & Carter, 2009; Marshall-Pescini et al., 2017; Borrego, 2020) (Fig. 2B-D).

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 quantity of food is distributed to the feeding box, which is closed by a sliding door with a strong magnet (Jenny & 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 & Schmid, 2002). Electronic feeders are available in all different shapes and sizes, such as electronic scatter feeders which are placed above the ground and scatter certain foods, e.g. pellets for bears randomly throughout the day (Andrews & 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 quantity 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 (Ziegeltrum & 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



Fig. 2: 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 (by Hare & Jones (2018); screenshot from an uncredited video no longer available on YouTube; (B) cooperation task in spotted hyenas; photograph from Drea & Carter (2009); (C) cooperation task in wolves; photograph from Marshall-Pescini et al. (2017); (D) cooperation task in lions; photograph from Borrego (2020).

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 (Law & Kitchener, 2002).

However, the methods mentioned above are not the only ones existing. Motivated, committed 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 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.

Materials and methods

This study was supported by the EAZA Felid TAG and Canid and Hyeamid TAG. We collected and compiled data from 44 zoos in 7 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 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 (*Acinonyx 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 find out what 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 during the visit. Some feedings could not be observed in person due to the presence of offspring, 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 report on 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 (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 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, 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. 3, Table 4). Large carcasses were used very rarely by the visited zoos; only 2 zoos used large carcasses on a weekly basis. The majority of zoos did not use large carcasses at all, or only very sporadically (Fig. 3A). By contrast, small carcasses were frequently used, with a majority of zoos using them at least once per week (Fig. 3B).

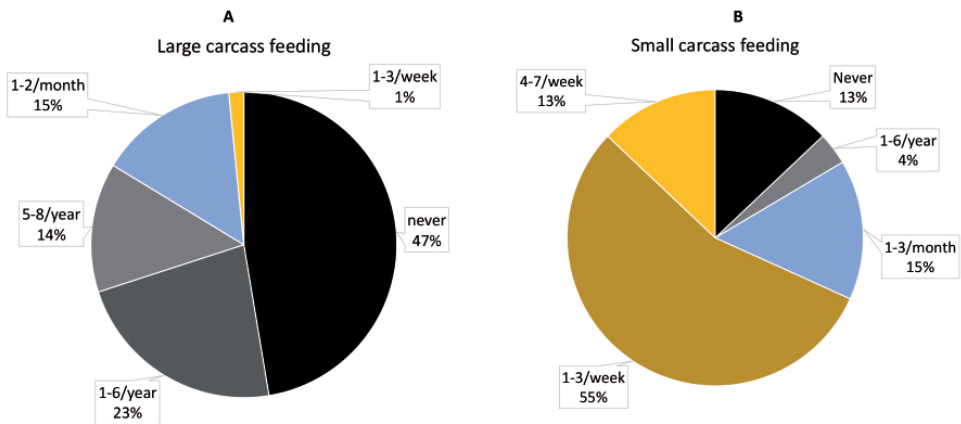


Fig. 3: Summary of the use of (A) large and (B) small carcass feeding for 11 species of large carnivores in 44 European zoos.

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.

Feeding option (Table 2)

The option of feeding each animal one portion 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 observed in two zoos. Scattering the food was reported by 68% of zoos with the majority using this option for brown bears (67%), 64% used the option of 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%, none of the zoos (0%) used this method in cheetahs, lynxes, hyenas and wolves.

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

Tab. 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%)

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 (Table 3)

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 used only 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 up the food 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%, hand feedings – 80%, swinging platforms and ziplines – 50%, hanging up the meal – 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 a third were zoos with tigers and a quarter 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% of institutions keeping hyenas). This was actually observed in 14% of institutions reporting this method. 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 had to detach the carcass while swimming (Fig. 1D). Across all species, half of the zoos either used only feeding loose on the ground and hand feeding or an additional method (Table 5).

Subjectively, the speed of consuming the meal was faster when feeding by hand or placing the food 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 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.

Tab. 5: Number 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%

Discussion

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

Carnivores in the wild are able to perform appetitive foraging 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 stereotypes (Jenny & Schmid, 2002). The option of using live prey to make offer a surrogate hunting experience to zoo carnivores, though possibly even accepted by a majority of zoo visitors (Ings et al., 1997; Lemmen et al., 2008), is not considered ethically acceptable in many instances because while increasing the welfare of animals (here: predators) is a clear aim, this should not be achieved by compromising the welfare of other animals (here: prey).

Therefore, other options are required to make feeding an important behavioural part of the day. 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 & 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 behavioural 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 large number of institutions that only used a very limited number of feeding methods; and 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. With 44 the number of zoological institutions was low compared to the overall number of EAZA zoos existing in Europe. Theoretically, a larger number of institutions 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 visit of the institutions, introduction to the animals and 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 used. Nevertheless, this finding emphasises that on average, these methods have not become part of the invariable routine in the participating zoos but are still being used 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 who is responsible for choosing diets, what feeding methods are available at the institution, and the actual 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 institutions. 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 within the scope of keepers' decisions. However, in the case of intended adjustments to a current dietary regime, all groups would have to work cooperatively to define a new goal and put it into practice.

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 muscles (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, 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 & Lindburg, 1990; McPhee, 2002; Cloutier & Packard, 2014). For example, Wood & Norris (2000) underlined the importance of recognising 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 & 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 & Lemon, 2001; McPhee, 2002; Gaengler & 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 behaviours and therefore helps avoiding monotony (Roe & 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). Additionally, these may be related to the fact that in many institutions, husbandry routines require a daily or even more frequent shifting of the animals between enclosures, which is traditionally being done by feeding certain (smaller) portions of food. 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 & Lemon, 2001; Gaengler & 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 civilisation, 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. Large carcass feeding represents a physical challenge for commissary personnel and keepers, and may not blend easily in the management systems of some institutions that depend on frequent shifting of animals currently accomplished by small portion feeding. Therefore, decisions to promote this feeding need to be flanked by measures that make large carcass feeding logistically feasible, possibly requiring – depending on the institution – different degrees of constructional, equipment, and animal management and training measures.

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 to a certain degree enhance visitor frequency or enhance motivation for visitors to acquire subscriptions, 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 zoological institutions. 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, Tables A1-11). 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 institutions. In particular, the lack of feeding methods that require cooperation of social carnivores (Drea & Carter, 2009; Marshall-Pescini et al., 2017; Hare & Jones, 2018; Borrego, 2020), appears as a lost opportunity, both in terms of the attractiveness and educative potential of exhibits and in terms of effects on the social cohesion of the animal group (Fig. 2).

Arguably, the most important feature of a planned feeding regime is the variety of methods employed. In this respect, some institutions 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 institutions employed feeding on the ground/by hand only or an 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 attractiveness 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 bottlenose 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. Notably, an actual document does not preclude variation or flexibility, as these aspects can be included in any procedure. A written management plan should 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 an institution commits itself to. In particular, the absence of a written document can easily be understood by many participants as a lack of priority, a viewpoint zoos might want to avoid. The process of developing such a plan might also point out changes in construction, equipment and management necessary to meet modern expectations of carnivore feeding.

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 institutions 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, or 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 (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.

Zusammenfassung

Die Lebenserwartung von Raubtieren in Zoos hat sich stetig verbessert; damit stellt sich die Frage, wie diese längeren Leben verbracht werden. Weil das Fütterungsmanagement einen besonderen Einfluss auf das Verhalten von Raubtieren hat, wurde die Fütterung in 44 europäischen Zoos in sieben Ländern im Rahmen von persönlichen Besuchen erhoben. Dies erfolgte, indem die verantwortlichen Personen während ihrer täglichen Routine mit elf Raubtierarten begleitet wurden. Fleisch an Knochen wurde von der Mehrzahl der Zoos eingesetzt; eine Ganzkörperfütterung wurde vorwiegend mit kleinen Futtertieren (Nager, Kaninchen, Geflügel) durchgeführt, aber kaum mit größeren Tierkörpern. Während viele Zoos ein bestimmtes Repertoire an Fütterungsmethoden mit unterschiedlichem Beschäftigungspotenzial angaben, wählten die meisten Zoos während der Besuche diejenigen Methoden ihres Repertoires, die als am wenigsten arbeitsaufwändig und als am wenigsten verhaltensanreichernd einzuschätzen waren. Die Zahl der Zoos, die nur ein begrenztes Repertoire an Fütterungsmethoden angaben, war unerwartet hoch, und publizierte Methoden wie 'swing pole feeders', an Laufseilen aufgehängte Beute, oder Selbstfütterungskästen (exkl. Zeitverzögerte Futterkästen, Tonnenfütterung bei Bären) wurden in keinem der besuchten Zoos eingesetzt. Außerdem wurden weder Methoden eingesetzt, die bei sozialen Raubtieren eine Kooperation der Rudelmitglieder erfordern, noch

Methoden, bei denen die Tiere scheitern könnten (die also eine erfolglose Jagd simulieren). Um die Zoohaltung großer Raubtiere natürlichen Gegebenheiten mehr anzunähern, empfehlen wir, vermehrt die Fütterung großer Tierkörper einzusetzen, verbunden mit physisch und kognitiv adäquat herausfordernden Aufgaben; dies erfordert ggf. entsprechende bauliche und organisatorische Maßnahmen. Der regelmäßige Einsatz von aufwändigeren Fütterungsmethoden könnte durch schriftliche Einsatzpläne gesichert werden. Dadurch würden sich alle Beteiligten vermutlich auch des damit verbundenen logistischen und zeitlichen Aufwandes bewusst, wodurch eine bessere Zeiteinteilung der Abläufe zur Versorgung der Tiere entstehen kann, genügend Zeit für den Einsatz aufwändigerer Fütterungsmethoden eingerechnet wird, und eventuell notwendige Veränderungen in Bau und Ausstattung angesprochen werden.

References

- Allen, M.E., Oftedal, O.T., & Baer, D.J. (1996). The feeding and nutrition of carnivores. Pp. 139-147 in: D.G. Kleiman, M.E. Allen, K.V. Thompson, & S. Lumpkin (eds), *Wild mammals in captivity: Principles and techniques*. University of Chicago Press, Chicago.
- Andrews, N.L., & Ha, J.C. (2014). The effects of automated scatter feeders on captive grizzly bear activity budgets. *Journal of Applied Animal Welfare Science*, 17, 148-156.
- Bond, J.C., & Lindburg, D.G. (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, I.L., Rödel, H.G., 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, T.L., & Packard, J.M. (2014). Enrichment options for African painted dogs (*Lycyaon 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.P.J. (2018). Predator size and prey size-gut capacity ratios determine kill frequency and carcass production in terrestrial carnivorous mammals. *Oikos*, 128, 13-22.
- Depauw, S., Bosch, G., Hesta, M., Whitehouse-Tedd, K., Hendriks, W., 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, 2540-2548.
- Depauw, S., Hesta, M., Whitehouse, Tedd, K., Vanhaecke, L., Verbrughe, 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, 146-154.
- Drea, C.M., & Carter, A.N. (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, K.A. (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, V.J., & Jones, M. K. (2018). Enrichment for physical fitness: let's get physical. Proceeding of the International Congress of Zookeepers, 18 (no page numbers).
- Höttges, N., Hjelms, 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.
- Ings, R., Waran, N. K., & Young, R. J. (1997). Attitude of zoo visitors to the idea of feeding live prey to zoo animals. *Zoo Biology*, 16, 343-347.
- 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, C.L.M., Clauss, M., Burkevica, A., & De Cuyper, A. Fasted and furious? Considerations on the use of fasting days in large carnivore husbandry. *Journal of Zoo and Aquarium Research* (submitted).
- Kroshko, J., Clubb, R., Harper, L., Mellor, E., Moehrenschrager, 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, A.C. (2019). Twenty years of the tiger feeding pole: review and recommendations. *International Zoo Yearbook*, 54, 174-190.
- Lemmen, W., van der Harst, T., Ophorst, S. & Huisman, T. (2008). Attitude of the general public towards feeding live prey. Proceedings of the European Zoo Nutrition Conference, 5, 30.
- Lindburg, D. G. (1988). Improving the feeding of captive felines through application of field data. *Zoo Biology*, 7, 211-218.
- Macdonald, D. W. (1996). Social behaviour of captive bush dogs (*Speothos venaticus*). *Journal of Zoology*, 239, 525-543.
- Marshall-Pescini, S., Schwarz, J. F., 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, M. E. (2002). Intact carcasses as enrichment for large felids: Effects on on- and off-exhibit behaviors. *Zoo Biology*, 21, 37-47.
- Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, 102, 246-261.
- Miller, L. J., Ivy, J. A., Vicino, G. A., & Schork, I. G. (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? International Conference on Environmental Enrichment. New York: Wildlife Conservation Society (no page numbers).
- Roller, M., Müller, D. W. H., Bertelsen, M. F., 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, E. K., Visscher, N. C., & Ha, R. R. (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 illustrated guide to their evolution and natural history*. New York: Columbia University Press.
- van Orsdol, K. G. (1984). Foraging behaviour and hunting success of lions in Queen Elizabeth National Park, Uganda. *African Journal of Ecology*, 22, 79-99.
- Veninga, S. A., & 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. <http://www.painteddogconservationininet.net.au/news/whole-carcass-feeding-by-veninga-and-lemon-2001.pdf>.
- Wagman, J. D., Lukas, K. E., Dennis, P.M., Willis, A., Carroscia, J., Gindlesperger, C., & Schook, M. W. (2018). A work for food enrichment program increases exploration and decreases stereotypies in four species of bears. *Zoo Biology*, 37, 3-15.
- Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, 33, 251-256.

- Williams, B. G., Waran, N. K., Carruthers, J., & Young, R. J. (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. Perth Zoo.
- Young, R. J. (1997). The importance of food presentation for animal welfare and conservation. *Proceedings of the Nutrition Society*, 56, 1095-1104.
- Ziegler, G. J., & Nolte, D. L. (1997). Black bear damage management in Washington State. *Proceedings of the Eastern Wildlife Damage Management Conference*, 7, 104-107.

Appendix

Tab. 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	personally observed using method)		Feeding option	personally observed using method)		Feeding method	personally observed using method)	
	use in number of zoos	(% zoos using method)		use in number of zoos	(% zoos using method)		use in number of zoos	(% zoos using method)
Minceed/ 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%)

Tab. 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	personally observed		personally observed		personally observed		personally observed	
	use in number of zoos	(% zoos using method)	use in number of zoos	(% zoos using method)	use in number of zoos	(% zoos using method)	use in number of zoos	(% zoos using method)
Mined/ processed meat	0	-	23	12 (52%)	Hand feeding	0	-	
Organs	6	0 (0%)	12	2 (17%)	Loose on the ground	30	12 (40%)	
Whole meat	5	2 (40%)	15	1 (7%)	Tried to the ground	18	4 (22%)	
Meat on bone	31	18 (58%)	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	-	

Tab. 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	personally observed		Feeding option		personally observed		Feeding method		personally observed	
	use in number of zoos	(% zoos using method)			use in number of zoos	(% zoos using method)			use in number of zoos	(% zoos using method)
Mince/ 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%)

Tab. 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 (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos 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	-

Tab. 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 (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Minceed/ 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	-

Tab. A6: Methods of cheetahs (*Acinonyx 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	personally observed (% zoos using method)		Feeding option		personally observed (% zoos using method)		Feeding method		personally observed (% zoos using method)	
	use in number of zoos	observed (%)	use in number of zoos	Feeding option	use in number of zoos	observed (%)	use in number of zoos	Feeding method	use in number of zoos	observed (%)
Mined/ processed meat	0	-	14	One pile for each	1	12 (86%)	1	Hand feeding	1	1 (100%)
Organs	3	0 (0%)	2	Hiding	15	1 (50%)	12	Loose on the ground	12	80%
Whole meat	3	2 (67%)	6	Scattering	2	1 (17%)	0	Tried to the ground	0	0%
Meat on bone	13	4 (31%)	0	Time-delayed dispensing	4	-	0	Hung up	4	0 (0%)
Whole meat with fur/feathers	5	0 (0%)			0			Hung up with counterweight	0	-
Carcass parts with fur/feathers	6	0 (0%)			1		1	Hung up elastic cord	1	0 (0%)
1/2 carcass	1	0 (0%)			0		0	Swinging platform	0	-
Complete eviscerated carcass	0	-			0		0	Woodpile feeder	0	-
Carcass without digestive tract	3	2 (67%)			0		0	Swing pole feeder	0	-
Decapitated carcass	2	0 (0%)			0		0	Self-serving feeder	0	-
Whole carcass	11	4 (36%)			0		0	Movement induced dispenser	0	-
					0		0	Feeding stick	0	-
					0		0	Pole feeding	0	-
					3		3	Run	3	0 (0%)
					1		1	Zip line feeding	1	0 (0%)
					0		0	Pulley feeder	0	-
					0		0	Wrapped in something/ hidden	0	-
					0		0	Novel objects / self-built	0	-
					0		0	Swimming	0	-

Tab. 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 (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos using method)
Mince/ 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	-

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

Tab. 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	personally observed (%)		Feeding option		personally observed (%)		Feeding method		personally observed (%)	
	use in number of zoos	using method)	use in number of zoos	using method)	use in number of zoos	using method)	use in number of zoos	using method)	use in number of zoos	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	-		
						Dug into ground	3	0 (0%)		
						Swimming	0	-		

Tab. 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 (% zoos using method)	Feeding option	use in number of zoos	personally observed (% zoos using method)	Feeding method	use in number of zoos	personally observed (% zoos 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%)
						Dug into ground	2 (1)	0 (0%)
						Swimming	6 (4)	1 (25%)

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

* According to keepers' advice, bears should be slowed down in feeding enrichment towards hibernation, therefore less different feeding methods could be personally observed

Tab. 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	personally observed		Feeding option		personally observed		Feeding method		personally observed																							
	use in number of zoos	(% zoos using method)	One pile for each	Hiding	Scattering	Time-delayed dispensing	use in number of zoos	(% zoos using method)	Hand feeding	Loose on the ground	Tied to the ground	Hung up	Hung up with counterweight	Hung up elastic cord	Swinging platform	Woodpile feeder	Swing pole feeder	Self-serving feeder	Movement induced dispenser	Feeding stick	Pole feeding	Run	Zip line feeding	Pulley feeder	Wrapped in something/hidden	Novel objects / self-built	Dug into ground	Swimming	use in number of zoos	(% zoos using method)		
Minced/ processed meat	0	-	One pile for each				12	5 (42%)	Hand feeding																					4	100%	
Organs	5	1 (20%)	Hiding				5	3 (60%)	Loose on the ground																					12	50%	
Whole meat	6	1 (17%)	Scattering				7	2 (29%)	Tied to the ground																					2	0%	
Meat on bone	7	1 (14%)	Time-delayed dispensing				2	0 (0%)	Hung up																					5	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%	
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%
									Pulley feeder																					0	-	
									Wrapped in something/hidden																						1	100%
									Novel objects / self-built																						3	0%
									Dug into ground																					0	-	
									Swimming																						3	33%

*According to keepers' advice, bears should be slowed down in feeding enrichment towards hibernation, therefore less different feeding methods could be personally observed

